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Tropical Blackwater Rivers, Animals, and Mast Fruiting by the Dipterocarpaceae

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ABSTRACT

It is proposed that tropical nutrient-poor white sand soils produce blackwater rivers, rivers that are rich in humic acids and poor in nutrients, because the vegetation growing on these soils is exceptionally rich in secondary compounds. The humic acids (= tannins and other phenolics) may even be only the more conspicuous of the secondary compounds that leach out of the living vegetation and the litter. While the water and the soil (including litter) may be expected to have a low productivity and animal biomass solely on the basis of its low nutrient content, it is quite possible that large amounts of secondary compounds are also debilitating to the animal community. An exceptionally high concentration of secondary compounds is expected in the vegetation growing on white sand soils for two reasons. First, this is an expected outcome in habitats where the loss of a leaf to an herbivore or through deciduous behavior is relatively a much greater loss than on nutrient-rich soils. Second, the plants growing there belong for the most part to families exceptionally rich in secondary compounds, a characteristic which is in turn selected for by the chemical defense requirements of plants growing in low diversity stands. The small amount of data that is available from Sarawak white sand habitats shows that the carrying capacity for animals is very greatly reduced. The postulated cause is reduced primary productivity and/or much of the productivity being used by the plant for secondary compounds (unharvestable productivity), or stored for seed crops at very long intervals (unavailable productivity). It is proposed that mast fruiting at the community level, as displayed by trees in the Dipterocarpaceae, is a mechanism of escape from seed predators that is unique to this part of the tropics (S.E. Asia) because this area has reduced animal communities (both on white sand soil sites and in general), and because the climate is sufficiently uniform for such an intra- and inter-population cueing system to evolve. Without experimentation, it is impossible to know, however, if the animal community is reduced solely due to overall lowered primary and harvestable productivity, or as well to the inevitable reduction in animal numbers when many of the trees in a habitat wait more than a few years for their highly synchronized seed crops. The occurrence of numerous tropical habitats with a very low diversity of trees inviolates the currently popular dogma that diversity is mandatory for stability in tropical habitats. I propose that the trees in such monotonous habitats are exceptionally well-protected chemically with respect to foliage, and have either very toxic seeds or well-developed mast cycles.

THE TROPICAL ECOLOGIST is confronted with four related questions:

- I) Why do some tropical habitats produce blackwater rivers?
- II) Why do these habitats contain drastically reduced numbers of animals?
- III) How is it that mast (= gregarious) fruiting has evolved at the population and community level in a group of lowland tropical trees, the southeast Asian Dipterocarpaceae?
- IV) How is it that certain lowland tropical trees persist in forests of very low species richness?

I wish to explore the idea that these are expected and ecologically related properties of habitats based on soils that are exceptionally deficient in nutrients. Each of these four questions is discussed as though it were a somewhat independent line of inquiry. However, I relate them in an attempt to generate a holistic evolutionary ecological viewpoint of tropical habitats with low productivity. It must be recognized from the start that this inquiry is largely intended to generate testable hypotheses and show that sufficient circumstantial evidence exists to make their proposal reasonable.

I. TROPICAL BLACKWATER RIVERS

Some lowland tropical river basins contain tributaries with water that is clear yet brown to nearly black in color. The Rio Negro of the northern Amazon basin is the largest and best-known tropical blackwater river (Ducke and Black 1953; Fittkau 1967; Klinge and Ohle 1964; Marlier 1965, 1973; Sioli 1955, 1964, 1967b, 1968a,b; Sioli and Klinge 1962; Sioli *et al.* 1969), but smaller bodies of blackwater occur in the southern Amazon (Sioli 1967a), various tributaries of the Congo (Clerfayt 1956; Doubois 1959; Marlier 1973; Rougerie 1958), Nigeria (Clayton 1958), Sarawak (Anderson 1963, 1964b; Ashton 1971; Inger and Chin 1962; Janzen 1974; Richards 1936, 1963), Malaya (Johnson 1967a,b, 1968; Mizuno and Mori 1970), East Indies (Polak 1933), Guyana (Carter 1934; Davis and Richards 1933, 1934), Suriname (Heyligers 1963; Stark, pers. comm.), coastal Brazil (Anonymous 1960), Guatemala (L. G. Brinson 1973; M. M. Brinson 1973), northern British Honduras (pers. obser.), and other sites (see Klinge 1968 for a thorough bibliography).

Blackwater rivers usually flow from podzolized white quartz sand soils (regosols, bleached sands) or peat swamps (Handley 1954; Klinge 1965, 1967, 1969; Richards 1941). Klinge (1965, 1968) esti-

mated that at least 4475 million hectares of the tropics are podzolized. If we may infer from the known cases (Klinge 1967), most of this soil is sandy and may produce blackwater rivers. The white sands are usually eroded from ancient aeolian or alluvial sandstones (Hardon 1936; Johnson 1968; Richards 1941, 1952, 1973; Sioli 1964; Sombroek 1966), though Heyligers (1963) feels that Suriname white sands may be formed *in situ* by leaching. For example, the white sand soils in the watershed of the Rio Negro are alluvial deposits eroded from the Roraima sandstone in interior Venezuela, northern Brazil, and the Guianas (Zinke, pers. comm.). In view of their secondary or even tertiary origin, high porosity (leading to rapid leaching by heavy tropical rain) and low ion retention properties, it is not surprising to find that they are probably the most nutrient-poor soils in the world when compared with tropical latosols and other soil types (Arens 1963; Hardon 1937; Herrera 1972; Heyligers 1963; Klinge and Ohle 1964; Mohr 1944; Mohr and van Baren 1954; Richards 1963; Sioli 1954, 1967b; Sioli *et al.* 1969; Stark 1970, 1971a,b; Webb 1968). In a recent review of Amazon river basin soils at several hundred sites, Zinke and Castro (1973) found white sand soils to contain half or less as much carbon as nearly all other soils, and consistently to be at the low end of the gradient of phosphorus, nitrogen, calcium, potassium, and sodium concentration. Ungemach (1969) concluded that except for iron, the concentration of nutrients in the water of the Rio Negro was equal to that in the rainwater of the region; which suggests that there are no nutrients being weathered from parent material in white sand soil ecosystems.

Tropical blackwaters are usually very acidic (pH between 3 and 4.5), contain many fewer inorganic ions than do clear, white, or muddy waters in the same drainage basin, have low oxygen content, have low light penetration, and contain high concentrations of dark brown "humic acids" (Anonymous 1972; Black and Christman 1963; Carter 1934; Fittkau 1967; Flores *et al.* 1972; Foldats 1962; Ghassemi and Christman 1968; Hardon 1937; Hutchinson 1957; Joachim 1935; Johnson 1967a,b, 1968; Klinge and Ohle 1964; Marlier 1965, 1973; Mizuno and Mori 1970; Mohr and van Baren 1954; Richards 1941; Roberts 1973; Schnitzer and Khan 1972; Shapiro 1957; Sioli 1954, 1955, 1964, 1967a,b, 1968a,b; Sioli *et al.* 1969; Waksman 1938; Williams 1968). However, I must stress early on that there are undoubtedly many kinds of blackwaters; and this situation may account for many of the exceptions to the statements to be made in the follow-

ing pages. The low nutrient content of blackwater rivers is partially explainable by the observation that the soil they drain is not being formed by the weathering of base-rich rock. The polyphenolic humic acids are also well-known chelating agents for inorganic ions, and may be preventing their uptake by plants. The low oxygen concentration is probably due to the lack of aquatic plants (see below), though it must be remembered that the surface of the water and water at rapids should be well oxygenated. The low light penetrance is due to the humic acids. While only circumstantial evidence is available, it appears that the high acidity of the water is solely due to organic (humic) acids. However, the folklore of the lowland tropics suggests that soil temperatures are so high that litter decomposition occurs too rapidly for the accumulation of humic material. However, blackwater rivers also occur at cool tropical high elevations, and there, usually issue from peat bogs just as they do in the mid-latitudes. We are then left with the question of why should there be a high concentration of humic acids in these rivers?

Before dealing directly with this question, let us examine the circumstantial evidence for the effect of humic acids on the organisms in blackwater rivers. While the humic acids are organic compounds and therefore surely susceptible to degradation by decomposers, they are phenolics and belong to that special ecological class of toxic organic compounds known generally as "secondary compounds" or "defensive compounds" (Levin 1971; Whittaker and Feeny 1971). They are thus expected to be generally toxic, difficult to degrade, and persistent to a greater degree than other chemical plant debris. We should also expect them to have a negative effect on the organisms in blackwater rivers.

What suggestion is there that the humic acids, and other secondary compounds, in the blackwater rivers are detrimental to the organisms in blackwater rivers? Blackwaters have long been suspected to be toxic to aquatic organisms by local people and field naturalists. The humic acids in blackwaters are polyphenolic compounds, compounds that are well known to be toxic to a wide variety of organisms (see below) owing to their propensity for forming insoluble complexes with proteins (Bate-Smith 1973a,b; Feeny 1968, 1969; Handley 1954; Ribereau-Gayon 1972). Johnson (1967b) found that 9 of the 15 species of fish in Malayan blackwaters are air-breathers or surface swimmers. Many of the fish in the upper Rio Negro and in Florida blackwaters are obligatory air-breathers (McNab, pers. comm.), and Carter's (1935) work on Guyana air-breathers

was with fish from blackwater streams. M. M. Brinson (1973) and L. G. Brinson (1973) have found that blackwater, forced out of the peat swamps at the west end of Guatemala's Lake Izabal by rainy season flooding, is highly toxic and repellent to the fish that live in the ordinary water of the lake. In Malayan blackwaters, almost all species of insects are air-breathers (Johnson 1968). The standard explanation for air-breathing by these aquatic organisms is the low oxygen content of the water, but it seems equally likely that protein-complexing humic acids should play havoc with the oxygen-exchange surfaces of gills. Levanidov (1949) reports that water slaters (*Ascellus aquaticus*) placed "in water from the upper layer of a peat bog" died within 24 hours. Dunson and Martin (1973) report strong toxicity to fish of the organic acids in blackwaters from a Pennsylvania bog. In both these cases death was attributed to the low pH, but that conclusion may be viewed as just another way of describing the toxic effects of the humic acids. Geisler *et al.* (1971) found that Amazonian clear-water Characidae and Cichlidae were able to survive in acidic blackwater once the humic materials had been filtered out, suggesting toxicity went beyond mere acidity. Lisk and his associates at Cornell University (pers. comm.) have found that the saponins washed from birch bark are responsible for the heavy spring fish mortality in the Black River in the New York Adirondack Mountains. In traveling on the Rio Negro, Spruce (1908: 270) pointed out that there is "the great advantage of voyaging on black waters, that no carapaná (or zanuedo, as the Spaniards call them) interrupts one's repose . . . and this I could do undisturbed [at night] by the insects which are the greatest torment to the traveler on the [white water] Amazon." While the absence of biting insects may be due to a shortage of prey for aquatic larvae, it may be due as well to blackwater being an unfavorable chemical medium for their larvae. It has been suggested by numerous people that in addition to humic acids, blackwater rivers may contain other phenolics, such as the phytoanalogs of insect hormones. The trees of blackwater river drainage basins are likely suspects to contain these compounds (see below), and phytoanalogs of insect hormones have been shown to be highly effective against mosquito and black fly larvae (Cumming and McKague 1973; Spielman and Williams 1966; Williams 1970), and acorn barnacle larvae (Gomez *et al.* 1973). In speaking of Amazonian blackwaters, Fittkau (1971) says "the whole region is free of Culicidae, except for those few forms which live in pockets of water trapped by epiphytic bromeliads";

however, he also says that these same waters are very rich in chironomid species.

The productivity of blackwater rivers is extremely low. This characteristic is usually attributed to the low nutrient level, or lack of trace elements, acting by themselves or in concert with the low oxygen and low light penetrance. Low pH is often included in this array, but that may in itself be viewed as a toxic effect of the humic acids. However, there are enough cases where one or more factor is nullified and productivity still stays low to make the humic acids (and perhaps other secondary compounds) quite suspect. For example, Carter (1934), on Guyana blackwater streams, says "the only characteristic in which the forest [black] waters differ from the [temperate zone] moor waters is their relatively high content of nutrient salts, which are typically present in small amounts in moor waters." He also noted that flowing blackwater streams are well oxygenated. In comparing an Amazonian white water lake with a blackwater lake, Marlier (1965) found a very small number of fish with few species and low plankton productivity in the blackwater lake; however, his tables show that the oxygen content is even higher in the blackwater lake than in the white water lake.

"The Rio Negro might be called the Dead River—I never saw such a deserted region" (Spruce 1908: 268). "For the human populations living along the banks of black-water rivers, these rivers always have the fame of being 'hunger rivers'" (Sioli 1968a). "Turtle are very rarely met with in the Rio Negro, but only on some of its lower branches" (Spruce 1908:275). "Leaving San Fernando the party took their famous short cut down the 'black' or coffee-coloured, mosquito-less rivers past Javita and the portage of Pimichin, entered Rio Negro . . . The return journey was made up the 'white' Rio Casiquiare, which connects the Rio Negro with the Orinoco, and is remarkable for the wildness of its banks and the blood-thirstiness of its mosquitoes" (Sandwith 1925). Roberts (1973) and Marlier (1973) report that the fish and invertebrate biomass is greatly reduced in Amazonian blackwater rivers as compared with other lakes and rivers in the Amazon basin. Patrick (1964) states that in the non-blackwaters of the Amazon basin "the number of species [of animals] were greater than in the acid [black-water] streams as is the case in temperate zone streams." Gessner (1964) states that phytoplankton productivity is very low in the Rio Negro. Malayan blackwaters have "very low standing crops of animals and plants . . . and must be regarded as unproductive" (Johnson 1967a). "Collections [of fish] from 24

[Malayan] blackwater habitats . . . comprise only about one tenth of the Malayan fauna. Thus the fish of blackwaters are very restricted in variety" (Johnson 1967b). In Malayan blackwaters, the standing crop of fish may be as low as 0.5 gm/m²; they feed almost entirely on material falling into the water, yet in this detritivore community, "microphagous organisms are mostly rare or absent" (Johnson 1968); Cladocera, annelids, rotifers, gastrotrichs, nematodes, and protozoans are rare (Johnson 1968). Algae are rare, except for a few species which are locally common, and "higher plants are likewise uncommon and often absent" (Johnson 1968). In a Malaysian non-blackwater stream, Bishop (1973) estimated the fish standing crop to be 18 gm/m² and the invertebrate fauna to be very diverse. Fish are "slow growing and stunted" in Wisconsin blackwater lakes fed from peat bogs, and fertilization does not completely eliminate the effect (Johnson and Hasler 1954; Stross and Hasler 1960). In Tasek Bera, a blackwater lake in Malaya, "detritus on the bottom was thick, but no benthonic animal was found on it"; it had reduced numbers of zooplankton, virtually no molluscs and only 5 species of fish, whereas 5 white water lakes in Thailand and Cambodia had 13 to 29 fish species (Mizuno and Mori 1970). When describing Amazonian blackwater rivers, Sioli (1968a) states that floating meadows, "the biotope of probably the richest community of aquatic animals which exist in all Amazonian waters," are very common on Amazonian white water rivers, yet are completely absent from blackwater rivers. "The black-water rivers, even the big black-water rivers with wide mouth bays, exposed with their whole surfaces to the solar radiation, have very little primary production of phytoplankton and of submerged higher water plants. . . ." ". . . many of those river-lakes are more or less blackwaters with very little phytoplankton development and . . . the true great clearwater rivers as e.g., the *Tapajos* and the *Xingu* develop even water blooms, in spite of the chemical poorness of the water" (my italics).

Sioli's comment on the Tapajos and Xingu emphasizes that it is not merely the low nutrients in blackwater rivers that lead to their low standing crops. Johnson (1967a) has pointed out that "somewhat surprisingly the calcium concentration in most of the [Malayan] blackwaters proves to be higher than in non-blackwater tree-country habitats and the highest value of all is for a blackwater stream." The low pH cannot be the only factor, as some Malayan blackwater streams flow from peat bogs and then through limestone areas that raise the pH above 6.0; these streams have snails, somewhat more insects

and more fish, but the fish are highly restricted to these waters rather than occurring in other basic waters as well (Johnson 1968). To attribute the effects in the previous paragraphs to low oxygen content and low light penetration does not answer why plants and animals are absent from the surface, and ignores the fact that they are abundant in tropical turbid rivers.

To return to our original question, I propose that the rainwater runoff into blackwater rivers is exceptionally rich in "humic acids," and probably other toxic organic compounds, because 1) the leachate from fresh vegetation and decomposing litter on these soils is exceptionally rich in phenols and other plant defensive chemicals, and 2) the poor soil leads indirectly, and high input of phenols directly, to a litter and soil community relatively incompetent at degrading these same secondary compounds. In short, this appears to be a situation like that described for the podzolization of Russian taiga soils. Here, the phenol-rich lower plants, conifers, and ericaceous shrubs produce litter out of which leaches a dilute but highly acidic organic solution, whose free acid groups are gradually paired with basic ions as they move down through the sand soil, resulting in a clean sand layer over a layer of precipitated polyphenols ("humus," Ponomareva 1969: 260). The same process is clearly the case with the formation of mor under phenol-rich plants at more temperate latitudes (Dimbleby 1962; Handley 1954). On tropical white sand soils, originally sand rather than derived by weathering ordinary rock, it is quite possible that there is even less basic material. In addition to precipitating out in a "giant podzol" or very hard ortstein (e.g., Heyligers 1963; Klinge 1967), most of the phenolics are then simply being leached into the streams in a highly active state, continuing to complex with proteins, minerals, and other compounds as they move through the ecosystem. There is no *a priori* reason to expect that the secondary compounds in the litter are produced *de novo* by the soil flora, even though they may produce some for the same protective reasons as do the higher plants, and alter the composition of secondary compounds while degrading or avoiding them.

HYPOTHESIS 1. There are no studies directed at the subject, but there are three areas of strong circumstantial evidence that the leachate from litter and vegetation over tropical lowland white sand podzols is exceptionally rich in toxic phenolics and other secondary compounds.

A). In a habitat that has extremely low primary productivity (see section II), yet a climate favorable

to animals year round, there should be very strong selection for plants that are exceptionally rich in chemical defenses. This is so for at least three reasons. a) The loss of a leaf or other part to an herbivore should lower the plant's fitness proportionately more than in more fertile habitats, because of the greater cost of replacing both the nutrients consumed and the damaged part in infertile habitats. Proportionately more of the plant's resources are thus expected to be spent on defenses. b) In a habitat with lower productivity, the plant should produce better-protected leaves as a consequence of selection for leaves with a longer half-life. The vegetation on tropical white sand soils is commonly evergreen even when there is a severe dry season (e.g., Brünig 1973; Heyligers 1963; Huinink 1966; Takeuchi 1961). A lower turnover rate of leaves lowers the inevitable losses of nutrients each time one leaf is replaced with another (and see Small 1972b). The more slowly the herbivore damage accumulates on a leaf, the longer it will be before the leaf must be replaced for internal economic reasons. The evergreen habit of trees on white sand soils, to be discussed later, may be viewed as an outcome of this adaptive behavior. As Ponomareva (1969) puts it when speaking of the Russian taiga, "coniferous tree species, each year shedding only part of their needles, perennial subshrubs, evergreen plants, etc., are all adaptive forms of live nature to conditions under which mineral nutrients are strongly leached out of the plant's environment." We may also note that evergreen leaves tend to have heavy waxy cuticles, material that may on the one hand be viewed as a contribution to the organic leachate in blackwaters and on the other hand as adaptive in minimizing leaching from living leaves in a habitat poor in nutrients. c) In habitats with low productivity and containing vegetation whose seeds escape from predators by extreme toxicity or mast fruiting (= gregarious fruiting), we find low species richness of trees and high aggregation (see below). This spacing pattern should be associated with selection for those species that are exceptionally rich in secondary chemical defenses, as the plant has no escape in space (Janzen 1970).

B). The plants that grow on tropical white sand soils (usually podzols) belong to families that are particularly rich in defensive chemicals. On Malaysian white sand soils (and their overlying peat swamps) the commonest woody plants (species and individuals) are in the Anacardiaceae, Annonaceae, Apocynaceae, Araucariaceae, Burseraceae, Casuarinaceae, Dipterocarpaceae, Ebenaceae, Ericaceae, Euphorbiaceae, Fagaceae, Guttiferae, Lauraceae, Legu-

minosae, Melastomataceae, Moraceae, Myrtaceae, Podocarpaceae, Rubiaceae, Sapotaceae, and Thymelaeaceae (Anderson 1961, 1963, 1964b; Ashton 1964; Brünig 1965, 1968, 1969a,c, 1973; Fox 1967; Meijer 1970; Richards 1936, 1952, 1973). A list of the families of trees over 12 inches in girth in a Sarawak peat swamp forest (Anderson 1961) could hardly be more foreboding to an herbivore (numbers of species in parentheses): Dipterocarpaceae (5), Thymelaeaceae (1), Leguminosae (1), Sapotaceae (3), Ebenaceae (1), Apocynaceae (1), Crypteroniaceae (1), Anisophylleaceae (1), Anacardiaceae (3), Annonaceae (5), Rubiaceae (1), Sterculiaceae (1), Myrtaceae (6), Rutaceae (1), Aquifoliaceae (1), Sapindaceae (2), Xanthophyllaceae (2), Guttiferae (6), Icacinaceae (1), Fagaceae (1), Euphorbiaceae (1), Oleaceae (1), Burseraceae (1), Chrysobalanaceae (1), Myristicaceae (1), and Meliaceae (1). On the extensive white sand podzol described in New Guinea by Hardon (1936), the vegetation was almost entirely of gymnosperms (*Araucaria*, *Dacrydium*, *Phyllocladum*, *Podocarpus*), Ericaceae, ferns, mosses, and lichens (1860 to 2400 m elevation). With the exception of Melastomataceae and Annonaceae, the wood and roots of plants in all these families are well known to contain large amounts of latex, essential oils, resins, tannins, and other phenolic or terpenoid defensive compounds (Ashton 1964; Bate-Smith 1962; Browne 1955; Burkill 1935; del Moral and Cates 1971; del Moral and Muller 1969; Foxworthy 1927; Harshburger 1916; Hon 1967a,b; Jackson 1957; Mors and Rizzini 1966; Ohtaki *et al.* 1967; Quisumbing 1935, 1951; Richards 1936; Senear 1933; Slooten 1952; Standley 1920-1926; Thapa 1968; Webb 1968; Whitford 1906; Whittaker 1970; Williams 1960; Willis 1966), and other toxic secondary compounds such as juvenile hormones (e.g., Mansingh *et al.* 1970; Ohtaki *et al.* 1967; Retnakaran 1970; Williams 1970 and included references), and high silicon concentrations (Burgess 1965; Jones and Handreck 1967; Menon 1956).

In Guyana, sandy podzols support forests where more than 40 percent of the large trees are Lauraceae (greenheart; *Ocotea* = *Nectandra*) or Leguminosae (*Eperua*; Davis and Richards 1933, 1934; Richards 1941, 1952). On the Rio Negro and other Brazilian podzolized white sand soils, *Eperua* spp. are among the most common trees (Ducke 1940; Sioli 1960; Sioli and Klinge 1962; Takeuchi 1961, 1962a). The *Ocotea* trees are renowned for being "more resistant than any other known timber to the attacks of insects and marine borers" (Davis and Richards 1933; Menon 1956), and "old logs and

stumps of greenheart (*Ocotea*) decay extremely slowly, lasting unchanged for many years" (Davis and Richards 1933). *Ocotea venenosa* also contains a very toxic vertebrate poison (Schultes 1969). *Ocotea* wood is rich in alkaloids (Menon 1956) and tannins (Gonggryp and Burger 1948), and greenheart has an alkaloid in the bark (Burkill 1935). The fallen leaves of *Eperua* are nearly black (presumably from tannins) and stain the soil brown to a depth of 25 cm (Davis and Richards 1934). *Eperua* resin (gum?) is produced in a quantity sufficient for commercial harvest (Ducke 1940; Mors and Rizzini 1966). The freshly cut wood "becomes sticky with exudations from ducts similar to those in pine," the "odor of fresh wood is rather acrid, suggesting creosote," and "the average life of an untreated [fence and telephone] pole is 20 years" (Aitken 1930). Sawdust of *Eperua* and *Ocotea* has a very depressant effect on fungal growth (Ernest 1936). On Guyana, Carter (1934) says "these black-water streams are popularly supposed to derive their colour from the decaying leaves of the Wallaba (*Eperua* spp.), and it is certainly true that many streams of this type flow from Wallaba forest." After *Ocotea*, the next most abundant trees in the *Ocotea* forest are *Pentaclethra macroloba* (Leguminosae), *Eschweilera sagotiana* (Lecythidaceae), and *Licania venosa* (Rosaceae). In Costa Rica, *P. macroloba* has extremely poisonous seeds, and the tannin-rich logs persist for many years on the forest floor (Hartshorn, pers. comm.). Its roots have a conspicuous layer of tannin-rich cells just inside the epidermis (D. Janos, pers. comm.); the roots of *Eperua*, *Mora* (see below) and *Peltogyne* (purpleheart, another South American legume with very resistant wood) are dark brown (Norris 1969) and probably for the same reason. *Eschweilera longipes* has wood so rich in siliceous deposits that marine wood borer mandibles are worn down when they attempt to bore into it (Menon 1956). There is no information on *Licania venosa*, but Rosaceae produce large amounts of cyanogenic glycosides, alkaloids, and saponins (Pammel 1911), and *Licania* is one of the few trees in Costa Rican deciduous forest with evergreen leaves.

In the Suriname *Dimorphandra* (= *Mora*) forests described by Stark (1970), Lindeman and Moolenaar (1959), and Heyligers (1963), on white sand soils, the leaves are highly resistant to decay and accumulate to depths of over 200 cm, while on adjacent latosols litter accumulates only to a depth of a few cm. *Mora* is well known for dark-reddish wood extremely resistant to decay and termites—thus its use for fence posts, railway ties, and bridges—

(Allen 1956; Gonggryp and Burger 1948). Stark's (1970) *Dimorphandra* forest generates a black-water river (Stark, pers. comm.) as does Heyligers' (1963). Spruce (1908: 304) states that the vegetation on a Brazilian white sand soil was primarily a caesalpinaceous legume tree (*Mora*, *Eperua*, *Copaifera*, *Hymenaea*, and other legumes famous for heavy resin and tannin production are caesalpinaceous legumes, Standley (1920-1926)) and a vegetation composed in great part of Myrsinaceae and Rutaceae, with the latter being used as fish poison. Ericaceae are frequently mentioned in the descriptions of South American vegetation on white sand soil (e.g., Ducke and Black 1953; Heyligers 1963; Huinink 1966; Takeuchi 1961, 1962a). Ducke and Black (1953) point out that the forest along white water rivers is "characterized by a high percentage of trees without distinct heartwood [(wood impregnated with secondary compounds)] or with softer wood than that of their congeners growing in the 'varzea' of the rivers of black water." Ashton (1964) states that on Brunei yellow podzols "the litter, whether dense or not, was largely composed of leaves showing signs of resistance to rotting . . . some tree species here, such as *Dipterocarpus globosus* and *Dryanobalanops aromatica* (Dipterocarpaceae), showed marked accumulation of litter below their crowns owing to their resistant fallen leaves."

C). At Bako National Park, a white sand and blackwater site in Sarawak (Anderson 1963; Ashton 1971; Brünig 1965, 1968, 1969a, 1973; Janzen 1974), I found virtually all the woody plants, from early second growth of kerangas forest ("Padang") to mixed dipterocarp forest to peat swamp (all on white sand), to have leathery leaves with a conspicuous resinous, acrid or aromatic odor or taste when crushed. In my experience in the tropics, foliage with such omnipresent potential toxicity is not characteristic of insolated foliage of tropical forest on latosols, and especially atypical for plants of secondary succession. As Brünig (1969c) stressed, the "fast-growing pioneer species" of good soils "are notably lacking in the secondary vegetation on podzols." These sclerophyllous leaves (Ashton 1971; Brünig 1965, 1968, 1969a,b) are smaller than expected in a lowland rainforest site and appear to have a life span of well over a year. Arens (1963), Ashton (1964, 1971), Brünig (1969a,b,c), Ferri (1960), and Richards (1952) have suggested that this morphology of foliage is characteristic of tropical white sand podzols, and Ashton (1964) demonstrated a high concentration of tannin in the leaves of 18 tree families on sandy soils in Brunei (northern Borneo).

The leaves at Bako closely resembled the leaves

of gymnosperms and *Magnolia* (Magnoliaceae), *Persea* (Lauraceae), *Gordonia* (Theaceae), *Myrica* (Myricaceae), *Lyonia*, and *Leucothoe* (Ericaceae) and *Ilex* (Aquifoliaceae), which constitute the cedar, cypress, and evergreen peat swamp forest vegetation of Florida and southern Georgia on white sand soils drained by blackwater rivers (e.g., Collins *et al.* 1964; Monk 1966, 1968). Foliage of these and similar plants is well known to be long-lived and slow to decompose (e.g., Monk 1971), and to be poisonous to vertebrates, and presumably insects, owing to alkaloids, tannins, and (presumably) other phenols (Forbes and Bechdel 1931; Harshberger 1916; Muenscher 1970; Pammel 1911; Southwood 1972). Heinselman (1963) described peat bog litter as "a variable mixture of complex organic compounds including celluloses, lignins, autins, waxes, resins, alkaloids, and pectins. . . ." Furthermore, "species of *Sphagnum* are unique among the peat building plants . . . in the strongly acid reactions of their remains (pH 3.0 to 4.5), and in their consequent resistance to microbial attack" (Heinselman 1963). The list of medicinal plants gathered by drug companies from the New Jersey pine barrens (a blackwater peat-bog swamp on coastal sand soil) reads like a medicine man's warehouse: emetic, purgative, stimulant, febrifuge, astringent, acid stimulant, sialagogue, errhine, bitter tonic, diuretic, nephritic, poisonous, demulcent, emmenagogue, irritant, rubefacient, carminative, nervine, insecticide, diaphoretic (Harshberger 1916).

HYPOTHESIS 2. Why should a high input of phenolics lead to a litter community of reduced competence, thereby allowing a high rate of organic movement into the streams? A variety of litter microorganisms can degrade phenolics ("humic acids") in soil and water (Alexander 1964; Evans 1947; Foster 1949; Henderson 1957; Hurst *et al.* 1962; McConnell 1968). However, they do it slowly, require a well-oxygenated substrate, and require accessory energy sources (Burgess 1965). As Burgess (1967) put it, "the decomposition of the phenolic polymers, lignin and humic acids, is not well understood. As yet no one has demonstrated an enzyme system capable of decomposing these substrates," and "humic acids under North American prairie soils have a mean residence period of about 1000 years." Fungal degradation of associated material is a common way of obtaining pure lignin (e.g., Brown *et al.* 1967). Handley (1954) concludes that mor soil (characteristically having phenol-rich litter that decomposes slowly and has a very reduced litter fauna) is "normally associated with a vegetation relatively

rich in phenolic compounds and of low base content which gives rise to a relatively acid litter layer." When speaking of the Russian taiga (coniferous forest with an understory of mosses, lichens, and ericaceous shrubs), Ponomareva (1969) stressed that the plant residues "have a high content of compounds which do not decompose readily—lignin, wax, resin, etc., and which include the 'inhibiting' substances (tannins, terpenes, etc.). The latter do not decay readily, and inhibit the decay of all other organic substances . . . there is a low level of microbiological activity, and the biological cycle of elements is slow. The main result is an accumulation of forest litter at the surface, and its being leached by atmospheric waters of mobile organic compounds." She even says (*ibid.*: 257) that like tropical soils, "the northern podzols of Russia, which under natural conditions are quite often overgrown with high-grade coniferous forests . . . after deforestation require systematic fertilizing to grow annual crops."

Since the selective pressures that result in secondary compounds favor highly toxic chemicals that are difficult for animals to digest, it is not surprising that they appear to be difficult to degrade. Newly fallen tannin-rich leaves (e.g., Fagaceae such as beech, oak, chestnut) have to be leached by rainfall for many weeks to the point where the litter community will readily feed on them (Anderson 1973; Burgess 1967; Cartwright and Findlay 1943; Heath and King 1964; Lutz 1928; Nykvist 1963; Shanks and Olson 1961). It is not surprising to find these compounds in soil (e.g., Burgess 1965; Burgess *et al.* 1964; Whitehead 1964) and to find them having a negative effect on the soil and litter organisms. They can have substantial negative effects on mycorrhizae (Brian *et al.* 1945; Gimingham 1972; Harley 1952), bacteria (Alexander 1964; Burgess 1965; Corbet 1935; Kendrick and Burgess 1962), whole plants (Yardeni and Evanara 1952), roots (Grümmer and Beyer 1960; Sherrod and Domsch 1970; Waksman 1938; Wang *et al.* 1967a,b), free-living fungi (Cartwright and Findlay 1943; Frankland 1966; Lutz 1928; Nierenstein 1934; Nykvist 1959), vertebrates (Arnold and Hill 1972; Glick and Joslyn 1970; Longhurst *et al.* 1968; Tamir and Alumot 1970), soil animals (Anderson 1973; Heath and King 1964), insects (Feeny 1968, 1969; Miles 1969), worms (Burgess 1965; Shanks and Olson 1961), and organisms in general (Levin 1971; Nierenstein 1934; Whalley 1959; Whittaker 1970; Whittaker and Feeny 1971). The blackish-brown polyphenol-rich ortstein deep in tropical white sand podzols characteristically lacks roots (e.g., Heyligers

1963; Huinink 1966; Joachim 1935). Heyligers (1963) notes that "on the [white sand] savanna it seems to take 50 years before the charcoal is decomposed, under forest conditions perhaps shorter"; in Costa Rican deciduous forest, charcoal after a fire is generally gone in much less than 10 years. One wonders if the slow growth rate of plants on African and Australian termite mounds and the slow rate of disappearance of these mounds (Lee and Wood 1968, 1971; Nye 1955) might be due to concentrations of secondary compounds in and below the nest. Leaf litter in temperate zones takes longer to decompose under evergreen tree species than under deciduous ones (Shanks and Olson 1961). Burges (1967), Corbet (1935), Farmer and Morrison (1964), Handley (1954), Mohr and van Baren (1954), and Ponomareva (1969) stress that tannins, lignins, waxes, and resins are difficult to decompose (witness amber, Langenheim 1973), and their accumulation may make the soil so acid (down to 2.7 in the A₀ horizon) that it is effectively sterilized.

The effect of these compounds will also be enhanced by 1) the initial low nutrient quality of the soil (making the microorganisms more dependent on the organic litter itself for nutrients), 2) the high acidity of the soil (making life difficult for nitrifying bacteria and causing the immediate loss of basic ions to them through competitive uptake by fungi and higher plants), 3) the low nutrient quality of the litter (owing to selection favoring more intense removal of nutrients from a leaf before discarding it when growing on low fertility sites), 4) the removal of proteinaceous nutrients by complexing with phenols (e.g., Alexander 1964; Corbet 1935; Feeny 1969; Handley 1954), 5) a low rate of input of litter owing to low primary productivity, and 6) the high water content of the soils (owing to flooding or continuous rain in some tropical sites), which minimizes the chance for aerobic metabolism. It is ironic that the soil type least able to deal with a high input of toxic phenolic compounds should be the one to receive the highest input of them. This soil-litter substrate probably receives a very high input of other defensive compounds as well.

Finally, the relative ineffectiveness of the litter community is also suggested by the accumulation of deep leaf layers and even peat bogs (submerged and elevated) on some tropical sandy podzols (Anderson 1959, 1961, 1963, 1964a,b; Ashton 1964; Bailey 1951; Browne 1955; Brünig 1964; Clayton 1958; Coulter 1950; Heyligers 1963; Klinge 1967; Mohr 1944; Mohr and van Baren 1954; Richards 1941,

1963; Stark 1970). To accumulate litter, as in temperate zone peat swamps, podzols, and mors, should require exceptionally toxic litter at the high temperatures and rainfall of the lowland tropics.

II. REDUCED ANIMAL COMMUNITIES

I have asked why blackwaters have high concentrations of organic compounds, and proposed the answer that they drain vegetation that is exceptionally rich in secondary compounds and growing on very poor soil. Further, I suggested that the high secondary compound concentration in these plants is the outcome of selection by herbivores in habitats with exceptionally low productivity. The short answer, then, to the question of why are terrestrial animal communities reduced in blackwater drainage basins is that the productivity is low and that what *is* produced is so rich in toxins as to be largely unharvestable. This section draws together the available information on productivity and animal communities on white sand soils.

I have been unable to locate published information on the gross primary productivity of plants on tropical white sand soils, on the amount of that production that can be harvested by animals, or on the biomass or turnover of animals supported by them. There are, however, some very suggestive cues from agriculture. Richards (1952) and Aitken (1930) state that agricultural attempts on British Guiana white sand soils occupied by *Eperua* forest have completely failed. The forest on Sarawak white sand soil is called "kerangas" which roughly translated means "soil on which you cannot grow rice" (Richards, pers. comm.). Stark (1971b) points out that "the [white] sands of the Amazon Basin do not appear to hold promise as areas rich for agricultural development," that "the Brazil sands had a few species of ants and termites, but no earthworms" (Stark 1971a), and that "... mammals are sparse in these forests ..." (Stark 1971a). Speaking of Suriname Amerindians, Heyligers (1963) says "for their fields they burn mainly forest growing on red loamy sands and heavier soils, rarely on white sand, on which they preferably build their houses." He then comments that in the white sand areas "no earthworms were found." In a study of Welsh earthworm distribution by habitat, Pierce (1972) found none in peat soils and 3 to 7 species in soils less rich in phenolic compounds. Vegetation on white sand soils that has been subject to disturbance is invariably described as stunted, scrubby, and poorly developed (Arens 1963; Eiten 1963; Ferri 1960; Heyligers 1963; Richards 1952; Sioli 1967a; Spruce 1908; Stark 1970, 1971a,b), implying a very slow

rate of regeneration. Nye and Greenland (1960) do not even mention white sand soils in their thorough review of tropical shifting agriculture, with the implication being that indigenous peoples have not used white sand soil for agriculture.

It is well known in agricultural practice that plants grown on nutrient-poor soils commonly contain less minerals than those grown on nutrient-rich soils. In Java, Hardon (1937) has shown that the foliage of *Dacrydium elatum* (a gymnosperm, Podocarpaceae) contains more than three times as much ash and about seven times as much calcium when grown on andesitic laterite soils as when grown on white sand soils. *Crudia amazonica* is a caesalpinaeous legume tree common to sites flooded by either black or white water rivers; where the trees are flooded by black water their leaves contain less phosphorous and potassium than where they are flooded by white water (Williams *et al.* 1972). Benzing (1973) found the rainwater stem flow off of *Taxodium* (a gymnosperm growing in pure stands in blackwater swamps on white sand soils in the southeastern United States) to be the lowest in nutrient content of a number of tree species, and noted that the nutrient content of epiphyte leaves (which are obviously growing in a very nutrient-poor site) is exceptionally low. Canadian bog evergreen plants have substantially less minerals in their leaves than do leaves of deciduous forest trees on upland sites (Small 1972). If such data turn out to be representative of wild vegetation, it may well be that, secondary compounds aside, the foliage of vegetation on white sand soil sites is of lower nutrient value per bite to a herbivore than from more fertile sites.

Aside from considerations of primary productivity, what the plant does with what it makes is likewise important here. Mast fruiting at long intervals and production of exceptionally toxic seeds (see section III and discussion) lower the productivity from the animals' viewpoint. In the case of mast fruiting, a major source of foods for rainforest animals is absent for intervals of several years. There are two reasons why foliage and seeds that are rich in secondary compounds should be of lower value even to the specialist that can feed on them. First, in detoxifying the compounds, the specialist will have to expend some of the nutrients obtained (Freeland and Janzen 1974); and witness the requirement of bacteria for an additional energy source if they are to decompose tannins (Burgess 1965). The "conventional wisdom" that pesticide-resistant strains of insects do not survive in competition with wild types is highly suggestive of this

phenomenon. Second, a higher proportion of the plant's primary productivity is going into defensive compounds rather than material that can be easily assimilated. As Kira and Shidei (1967) have emphasized in their review of tropical primary production, two well-developed rainforests of the same biomass may be produced by widely different rates of primary production; even the tall and mixed dipterocarp forest growing on the white sand hillsides at Bako (see below) can be produced and maintained by very low primary productivity and therefore have very little harvestable productivity for animals.

In addition to the above indirect evidence, three recent studies in Sarawak partly document the very low animal biomass and suggest low harvestable productivity of vegetation growing on white sand soils.

BAKO: The habitat that I examined ranged from kerangas forest (with its secondary, or "padang" vegetation) on the top of 100 m tall and flat-topped sandstone hills, down to peat swamp forest in the valley bottoms near sea level (Bako National Park, on the coast of the South China sea, near Kuching, Sarawak, Malaysia; see Anderson 1963; Ashton 1971; Brünig 1965, 1968, 1973; Janzen 1974 for a more detailed description). On the equator (1°6' N, 110°5' E), Bako receives 3 to 4 m of rain, which is distributed quite evenly throughout the year. The scrubby and obviously disturbed (see below) "padang" vegetation on the hilltops was 1 to 4 m tall and contained nearly pure stands of the small tree *Ploiarum alternifolium* (Bonnetiaceae), with taller scattered shrubs and trees such as *Tristania*, *Whiteodendron*, and *Rhodamnia* (Myrtaceae), *Calophyllum* (Guttiferae), *Cratoxylum* (Hypericaceae), and *Dacrydium* (Podocarpaceae). When undisturbed, the hilltops supported a dense forest of 10 to 20 m tall trees in these families and those listed in the previous section for vegetation on white sand soil (Brünig 1968, 1973). Interspersed with the secondary vegetation were large areas (several were more than one-half hectare) of bare black hardpan, which was a B horizon left after erosion of the sand; this black ortstein was more than 1 m thick in places (fig. 1). The hillside forest looked like ordinary lowland tropical rainforest (= mixed dipterocarp forest of Brünig 1973) and was rich in Casuarinaceae, Dipterocarpaceae, Euphorbiaceae, Guttiferae, Lauraceae, Myrtaceae, and Podocarpaceae, and graded into the peat swamp forest described by Anderson (1963) in the valley bottoms.

1) Despite the total (and apparently effective



FIGURE 1. (A) Interface between hardpan (ortstein) exposed by erosion of white sand soil, and kerangas forest on the tops of the hills at Bako National Park. (B) 60-cm-tall ortstein boulder left behind following erosional fragmentation of a continuous hardpan such as that in A above. The vegetation around the boulder represents 30 years of undisturbed secondary succession following clearing by fire and cutting.

prohibition of hunting in the Park for at least 15 years (Anderson, pers. comm.), small vertebrates were extremely rare. In 11 days of working in the forest and along its edges, I saw only one arboreal (Geckonidae) and one terrestrial (Agamidae) insectivorous lizard, despite intensive search for 4 days. In structurally comparable vegetation and weather in Central America, the count would have been in the hundreds. During the same period, each morning I saw only 3 to 5 birds of all sizes in the forest and along its edges; birds were so scarce that each one caused special notice. At a similar site in Central America, the bird count would easily have been in the hundreds. The absence of bird calls was deafening; Ashton says that *kerangas* forest can be defined by its silence (Richards, pers. comm.). "Most of the forest areas of Bako appear to have a rather impoverished bird fauna, particularly so the *kerangas* areas" (Rothschild 1971).

Each day at the site, I walked about 5 km through secondary and primary forest on a wet white sand path (fig. 2A); in 10 days I saw the tracks of only one large felid and no other mammals. No rodent runways were found in the old field mentioned below, and the only sign of small mammals in the forest was two nuts that had been chewed open by a rodent. One squirrel was seen in the forest in 11 days. Harrison (1965) says of Bako, "the observer may find less than one mammal per 5 acres, and only perhaps 1 bird per acre, with frogs and reptiles correspondingly rare." For 3 days a 200-gram piece of canned ham remained untouched on the side of the creek through the old field. Aside from the pseudobulbs of orchids, in the Central American tropics, fleshy (starchy) storage tubers are found above ground on plants only in habitats where rodents are very rare: tops of high mountains (e.g., *Macleania* (Ericaceae) in Costa Rican cloud forest), and on Caribbean islands. At Bako, such tubers were conspicuous on three genera of epiphytic ant-plants and several species of vines (Janzen 1974).

Pieces of canned meat placed as ant bait in the hillside and secondary forest sometimes lasted as long as 24 hours without being found by ants (Janzen 1974); in any lowland Central American forest, such baits would remain undiscovered only a few minutes (unpub. field notes). In Suriname, Heyligers (1963) says "in the white sandy soils, especially in those of the open savanna and of the savanna scrub, animal activity is very restricted . . . in savanna wood and in savanna forest sometimes low broad sandheaps are found round the entrances of the nests of leaf-cutting ants, *Atta* spp. These ants,

however, are more often met in forest on red sandy loam."

Though no sweep samples of foliage-inhabiting insects were taken, my past experiences following a sweep net about in tropical vegetation (Janzen 1973a,b; Janzen and Schoener 1968) lead me to believe that the biomass of foliage-inhabiting insects would be about the same as on a Caribbean island or a 3000 m Costa Rican mountain top, i.e., 1 to 10 percent of that in the Costa Rican lowlands (assuming that comparisons are made between similar ages and types of the vegetation). At night, insects on the foliage were almost non-existent at Bako. I found only two termite nests in the vicinity of the site; similar searching in lowland Costa Rica would have yielded hundreds of termite nests. Flower-visiting insects were conspicuously rare even on the large flowers of *Ploiarum* (the commonest shrub in the secondary regeneration). I saw only one *Xylocopa* and two *Nomia* bees in 11 days. Only one social wasp nest was seen in the same time period, and that was in a mangrove swamp. At least two of the most common trees were wind-pollinated gymnosperms (*Casuarina*, *Dacrydium*). The prevalence of wind pollination, coupled with supra-annual flowering and fruiting by the common Dipterocarpaceae, indicates a distinct shortage of sugar and edible plant parts for both litter organisms and larger animals, as compared to an African or neotropical forest where the annual fruit input can be very high (Klinge and Rodriguez 1968; Smythe 1970). For example, *Spondias mombin* (Anacardiaceae) may produce as much as 5 tons (fresh weight) per hectare of fruit and seed in its annual fruiting in Panamanian rainforest (Hladik and Hladik 1969).

However, very large vertebrates were present, at least near the coastal river mouths. Brush-lipped pigs (*Sus*) rooted up the disturbed vegetation on delta clay soils near the Park buildings. A troop of macaques (*Macaca*) foraged intensely around the Park buildings, and a troop was seen twice in the hillside forest. Proboscis monkeys (*Nasalis*) have been seen in the mangrove swamps of the Park, and orangutangs (*Pongo*) have been trapped in the Park in the past (Anderson, pers. comm.). I saw one large deer (Cervidae) and one hornbill (Bucerotidae) near the beach. It is noteworthy that these are animals that can move long distances between local excesses of food and have a reputation for doing so (see section III), and probably can survive for long periods with little food (Bourliere 1973). A large varanid lizard foraged in the Park building garbage, and another was seen on the beach scavenging among beach litter. The above account would



FIGURE 2. (A) In front of Dr. Morrow is kerangas forest lightly disturbed a long time ago and in the foreground is 30-year-old secondary succession following clearing by burning and cutting. The (Lintang) trail was last scraped clean of vegetation four years earlier and has no regeneration despite use by no more than one or two persons a month. The site is about 500 m east of the site in figure 1A. (B) Looking to the right a few meters behind Dr. Morrow through 30 years of undisturbed secondary succession. The X is two meters above the ground.

be far richer in species and individuals in a similarly undisturbed rainforest site in the Central American lowlands.

2) The rate of regrowth of destroyed vegetation was extremely low. Patches totalling about 30 hectares of hilltop forest had been cut and burned to ground level, but not plowed, planted, or grazed, about 1942-1944 (information from local inhabitants near the Park); by 1972, the regeneration was only 1 to 2 m tall, with scattered trees as tall as 3 to 4 m (fig. 2). Heyligers (1963) describes a dirt road built in the 18th century across a white sand savanna: "Where this ancient road passes through the savanna, it is still easily recognizable, but where it penetrates into the forest, [on loams and latosols] it is entirely overgrown."

The low rate of secondary succession is probably due to a low immigration rate of tree seeds (owing to a lack of dispersal agents) as well as to a low growth rate of established plants. In African and neotropical evergreen lowland forests on latosols, there are numerous fruit- and seed-bearing shrubs and vines in the understory and forest edges. They fruit through much of the year, e.g., Heliconiaceae, Marantaceae, Melastomataceae, Palmae, Passifloraceae, Piperaceae, Rubiaceae, Solanaceae, Tiliaceae, etc. (and see Snow 1962, 1965), and one can find a couple of dozen species of forest trees in fruit at any time of the year, to say nothing of the peak fruiting times such as described by Foster (1973); Frankie *et al.* (1974); Janzen (1967); and Smythe (1970). At Bako there were almost no plants in fruit or flower in the forest and on its edges, implying an overall lower rate of seed generation by the forest, epitomized by the highly intermittent one of the Dipterocarpaceae. This absence of fruit and seed crops is probably one of the causes for the general absence of birds and small mammals in the forest, since fruits and seeds intended for proper dispersal agents constitute a large part of the diet of seed predators.

3) Human use also implies a low productivity by the habitat. Prior to establishment of the Park about 1959, paddy rice was grown only on the deltaic river bottoms near the ocean. While the art of growing dry-land rice on forest soil is well developed in Borneo (Freeman 1970), the farmers at Bako never cleared the forest on white sand hills for agriculture.

4) Several aspects of the extant vegetation also suggest low primary productivity. Lowland evergreen rainforest in the new world tropics is generally dotted with trees just putting out an entire new leaf crop or with flushes of new leaves in crowns already filled with older leaves. The evergreen forest in the Park

had the lowest incidence of such leaves I have ever seen in lowland tropical rainforest, and this was true for the understory as well as the canopy.

The life forms of the plants also suggest slow growth by the vegetation. The success of the vine life form clearly depends on its ability to grow rapidly in length. The biomass of vines is disproportionately reduced in tropical habitats where the absolute growth rate is reduced for all plants, such as at elevations above about 2000 to 2500 m, and in deserts. Vines are likewise extremely scarce at Bako, even in the secondary vegetation and forest edges. Their general absence on white sand soil sites has also been noted by Richards (1952). Furthermore, annual plants were almost entirely missing from the secondary succession. These small plants likewise depend on fast growth for survival in the face of competition with woody plants (usually in the early stages of succession). The absence of annuals on the white sand soils was especially conspicuous because at least 5 percent of the soil surface in the old cleared area was free of vegetation, despite the long time since the last disturbance. It is interesting in this context to note that while tree foliage commonly contains tannins, the foliage of annuals and other herbaceous plants is generally free of tannins (Bate-Smith 1973b; Feeny, pers. comm.).

5) The only fern and angiosperm epiphytes that could survive on plants growing on white sand soil at Bako were those with an exceptional method for obtaining food. Almost all epiphytes were associated with an *Iridomyrmex myrmecodiae* ant colony (fig. 3): four of the epiphytes (*Dischidia*, *Hydnophytum*, *Myrmecodia*, *Phymatodes*) were grown and fed by the ants, and the remaining epiphytic associates parasitized the system by rooting in the myrmecophytes' food (Janzen 1974). I found only 5 individuals of non-mutualistic fern epiphytes. These (e.g., *Drynaria*) had leaves modified for capturing falling leaves and other debris, and/or for harboring ants.

I interpret the shortage of ant-free epiphytes to be a consequence of a low rate of inorganic ion input to tree crowns from bird feces, insects, rain, dust, and falling leaves and twigs. Ungemach (1969) postulated that the extraordinarily low amount of plant nutrients in the rainwater falling in the Rio Negro river basin in Brazil was due to the low nutrient content of the soil. The postulated high concentration of phenols and other secondary compounds in leaf and bark leachate may also be of importance in regard to absence of epiphytes. The tannin-rich young bark of mangroves (e.g., Burkill 1935) is extraordinarily free of epiphytes in the neotropics

even when the soil adjacent to the mangrove swamp is of high quality. While not epiphytic, the extreme abundance of the insect-capturing pitcher plants (Nepenthaceae) and sundews (Droseraceae) also implies a strong competitive advantage for terrestrial plants with special nutrient-gathering devices.



FIGURE 3. (A) *Hydnophytum formicarium* Jack, myrmecophytic epiphytes growing on a tree in the kerangas forest in figure 2A. (B) *Myrmecodia tuberosa* Jack, another myrmecophytic epiphyte in the kerangas forest in figure 2A, and its ant occupants (*Iridomyrmex myrmecodiae* Emery). These ants appear essential for epiphyte survival in this nutrient-poor habitat (see text and Janzen 1974).

The conspicuous paucity of legumes at Bako is somewhat perplexing in this respect, except that acid soils appear to be particularly harsh for root-nodule bacteria (Alexander 1964). Brünig (1969c) states that "mycorrhiza and root nodules are conspicuously more frequent in [Sarawak] tropical podzols than in red-yellow podzolic or lateritic soils." Ashton (pers. comm.) disagrees with Brünig on this point, but Stark's (1971a, b) studies that emphasize the importance of mycorrhizae in tropical forest were done on Brazilian podzols (and see Huinink 1966; Klinge 1973). Stark (1970) also states that mycorrhizae appeared to be more abundant in Suriname white sand soil than in adjacent lateritic soils. However, Norris (1969) found no root nodules on *Eperua* and *Mora* (Leguminosae) on sand soils (but they did have well-developed mycorrhizae). As well as becoming increasingly important as soil nutrients become rarer, an association with phenol-resistant mycorrhizae might be one of the specializations possible for a tree with phenol-sensitive root hairs. Plants that shed large amounts of phenols and other secondary compounds onto their roots may need mycorrhizal associations to avoid self-intoxication. The mycorrhizal fungi, which are functionally serving as root hairs for the plant, may be specialists at resisting or avoiding these compounds. We know that some fungi do live on tannin-rich substrates. In this connection it is of interest that not only do *Mora*, *Eperua*, and *Pentaclethra* have thick roots with extensive mycorrhizal associations, but *Hymenaea courbaril*, which is famous for heavy resin deposits beneath the single trees (see section IV), does likewise (Janos, pers. comm.). It is probably not an accident that Stark developed her direct nutrient-cycling hypothesis in white sand with a phenol-rich litter.

6) Rain pools and creeks running off the sandstone hills and hardpan were virtually devoid of animal life. No fish were seen in the creeks at Bako, and no riparian fishing birds such as herons were seen near them. I found 2 dragonfly larvae (Odonata) and a few caddisfly larvae (Trichoptera) in hours of turning rocks and searching stream bottoms. When it rained, the streams produced thick mats of white foam at the bases of waterfalls, suggesting a high saponin content in addition to whatever organic compounds turned them dark brown.

7) The very large numbers of individuals of a few plant species (low species richness and low equitability of species abundances) in the secondary succession (and see Brünig 1973 for a description of equally low values for undisturbed forest) suggest a very harsh environment (and see below with

respect to reptiles and amphibians). Shortage of food for both plants and animals is probably the cause. In the secondary succession, there were many acres where more than 80 percent of the vegetation biomass was tied up in one species of sedge (Cyperaceae), *Tectaria borneensis* (Aspidiaceae), *Ploiarum alternifolium* (Bonnetiaceae), *Nepenthes gracilis* (Nepenthaceae), and ant-plants (primarily *Myrmecodia* and *Dischidia*), and the remaining vegetation contained a maximum of about 25 species of plants. *Iridomyrmex myrmecodiae* was the only arboreal ant found in the secondary succession by baiting and collecting, and its colonies occupied or foraged over at least 90 percent of the woody vegetation. On the ground, the same ant and a large black *Crematogaster* occupied 96 percent of the foraging area (as determined by their harvesting of baits placed on the ground, Janzen 1974). In the forest, the distribution of ant biomass was almost as badly skewed in favor of *Iridomyrmex myrmecodiae* and *Camponotus* as in the open.

Numerous workers (e.g., Ducke and Black 1953; Heyligers 1963; Klinge 1968; Richards 1952; Takeuchi 1961, 1962a,b) have stressed the same low plant species richness and equitability on South American white sand podzols, even in apparently undisturbed forest.

FOURTH DIVISION, SARAWAK: As part of herpetological studies in Borneo (Lloyd *et al.* 1968 and included references) Robert Inger collected frogs, lizards, and snakes in forest on white sand soil with blackwater creeks (Nyabau), hill forest (Pesu), and alluvial forest (Labang). The podzol site has "low forest with a thin canopy . . . typical heath forest as described by Richards (1952)" while the others are "tall with a dense canopy" and produce streams with clear or turbid water (Inger, in litt.). Working with a team of collectors, Inger obtained an average of 20.5 and 24.1 reptiles and amphibians per day at Labang and Pesu during 120 and 131 days of collecting, respectively; at the white sand site, they caught 17.8 per day. While these differences in numbers of individuals do not appear dramatically different, analysis at the species level is much more revealing. On the white sand site, there were 24 frog, 13 lizard, and 13 snake species, while at Labang and Pesu, the comparable figures are 33, 33, and 38 (plus 2 turtles) and 53, 31, and 35 (plus 1 turtle), respectively. Labang and Pesu, with 106 and 120 species of herps respectively, are more than twice as species-rich as Nyabau (50 species). It is probably significant that snakes, representing tertiary consumers for they eat almost entirely vertebrates (e.g., Arnold

1972), are the most reduced of all on the poor site. Frogs were the least severely reduced in numbers of species. If I may use my own unpublished experience with gut analyses of Central American frogs and lizards for documentation, frogs normally eat much smaller amounts of insects per unit body mass than do lizards, suggesting that frogs may maintain a higher biomass or species richness on less food than lizards.

The habitat specificity of frogs, lizards, and snakes was also instructive with respect to productivity. Of the 50 species in the white sand habitat, 92 percent are found in one or both of the other two habitats. Of the 106 and 120 species at the other sites, only 37 and 33 percent were found in the white sand habitat. This is precisely the trend of habitat-fidelity that would be expected of a carnivore if the white sand site has a much lower productivity than the other two sites. The different trophic levels show the same trend; while 74 and 77 percent of the snake species at the good sites were not found in the poor site, only 64 and 65 percent of the lizards and 48 and 60 percent of the frogs at the good sites were missing from the poor site. Again, the direction of this difference between frogs and lizards is expected if we recognize that frogs probably need fewer insects per animal per day than do lizards. It is of interest in this context that many of the trees found on white sand podzols are also found growing on yellow podzol and latosols, but the reverse is not true for many of the species that grow on the more fertile sites (Ashton 1964; Richards 1936).

PEAT SWAMP FOREST: The peat swamp forests in Brunei and Sarawak are notorious for their lack of conspicuous animal life, and in the center of a large swamp, there is almost complete silence. The over-story trees, primarily the dipterocarp *Shorea albida* (Anderson 1964a; Brünig 1964), are stunted. Dead snags are conspicuous, suggesting a slow rate of dead wood turnover, and when lightning strikes in the center of this vegetation the dead trees may stand for many years (Anderson 1964a; Brünig 1964; Richards, pers. comm.); a photograph in Anderson (1961) shows that one third of the *Shorea albida* trees killed by insect defoliation in a peat swamp are still standing 10 years later.

At Bako, there were small peat swamp forests slightly inland from the river deltas. A night collecting trip in this forest for animals of any sort or size was generally a waste of time. Calling frogs were very rare, and insects were seldom encountered on the foliage. In Central American swamps lacking

peat accumulation, animal life is very abundant. It seems safe to assume that a peat swamp represents hardly more than an extremely concentrated black-water river, where the breakdown of secondary compounds is further impeded by lack of oxygen. Such a site should display extremely low productivity harvestable by animals.

III. MAST FRUITING BY DIPTEROCARPACEAE

I have proposed in the previous two sections that leaves with exceptionally high concentrations of defensive chemicals are a consequence of the strong selection for anti-herbivore defenses in habitats with a climate favorable to animals yet with very low primary productivity, which in turn leads to low numbers of animals. In this section I wish to explore the hypothesis that mast fruiting by Dipterocarpaceae may be an indirect consequence of low productivity and low animal numbers. I will restrict my discussion for the most part to Sarawak and Malaya, as these are the only areas with reliable information on fruiting phenology.

Mast fruiting (called "gregarious fruiting" in much southeast Asian literature) by Dipterocarpaceae is behaviorally very similar to the supra-annual sexual phenology displayed by many North American and European canopy-member trees (e.g., *Abies*, *Carya*, *Fagus*, *Pinus*, *Quercus*, *Tsuga*). The latter trees have population- and community-level fruiting that is synchronized at intervals of greater than one year. The adaptive significance of being synchronized to the individual tree is clearly the advantage of fruiting when seed predators have been satiated (Janzen 1971). In Sarawak, Brunei, and southern Malayan lowland and hill evergreen rainforest, it is well known that most individuals in many dipterocarp genera (e.g., *Cotylelobium*, *Dipterocarpus*, *Dryobalanops*, *Hopea*, *Parashorea*, *Shorea*, *Vatica*) fruit synchronously over tens of square miles at 5- to 13-year intervals (Ashton 1964, 1969; Burgess 1968, 1969; Fox 1967, 1968; Medway 1972a; Meijer 1970, 1973; Wood 1956). For example, Wood (1956) reported that more than 100 species of Dipterocarpaceae flowered, and presumably fruited, in Sabah, Brunei, Sarawak, and Indonesia in 1955. While detailed data are not available, Ashton (1969) stresses that "along with them many other families flower unusually heavily."

Individual temperate-zone mast-fruiting trees that fruit out of phase are heavily selected against (Janzen 1971), and the same happens to dipterocarps that are out of phase. "Sporadic flowering and fruiting of economic species [of Dipterocarpaceae] occurs

somewhere in the [Malay] peninsula every month, but it is seldom of much value and the fruit is likely to be almost completely destroyed by insects, birds or animals" (Wood 1956). Ashton (pers. comm.) has stressed that insects and vertebrates take a very heavy toll of dipterocarp seeds except in mast years. I should point out, however, that just as we can no longer examine the coevolution of the passenger pigeon (the primary acorn predator) and mast fruiting by oaks in North America (Janzen 1971), the reduction of big mammal populations in Malaya and Borneo by hunting makes this question very difficult to examine directly.

Physiologically, mast fruiting probably involves little more than storage of photosynthate until it accrues to the amount needed to produce a seed crop of a size that accomplishes seed predator satiation. Once this level is reached, we may expect the tree to become physiologically sensitive to an external weather event that will be likewise perceived by other dipterocarps. This flowering cue appears to be a period of several rainless weeks in the case of Sarawak, Brunei, and Malayan rainforest dipterocarps (Ashton 1964, 1969; Medway 1972a; Meijer 1970; Poore 1964, 1968; Wood 1956). On an annual basis, a milder version of this same cue is used by some Malaysian bats to synchronized reproduction (Medway 1972b). With such a system we may expect cyclic fruiting at long intervals, even when notable dry spells occur at more frequent intervals. It is not surprising, then, to find, as Wood (1956) did, that fruiting years are not drier than most dry years. Ecologically and evolutionarily, the question is much more complicated than physiologically. We are confronted with four interrelated questions. 1) Why is population- and community-level mast fruiting an effective reproductive strategy for trees in these particular tropical forests? 2) Why do these trees store photosynthate for such a long time before responding to the flowering cue of a dry spell? 3) How did this behavior evolve? 4) Why did this defense mechanism appear in the Dipterocarpaceae, rather than in some other family of trees?

1) Why is mast fruiting effective in Malayan and Bornean rainforest? The short answer has to be that the animal community is in some sense smaller there than in other lowland tropical forests, such as those of Africa and the neotropics. In these latter areas, there are no reported cases of population- or community-level mast fruiting and no suggestion of their existence from the field experiences of tropical biologists whom I have consulted. Seed predator satiation occurs at the level of the individual tree's seed crop and annually at the population level in all

tropical areas, but southeast Asia is unique in having a large number of tree species involved in predator satiation by fruiting synchrony at greater than one-year intervals. The critical trait of a mast crop is that there must be so much seed that all the seed predators that find it cannot kill the seeds before some are dispersed or grow to a relatively immune stage. In temperate-zone forests, this excess of seed over animal destruction capacity occurs because inclement weather takes a heavy toll of the animal populations between large seed crops. Furthermore, because there are a small number of tree species, most individual trees are involved in mast fruiting, and therefore there are few seeds and fruits available for animals in the years between crops (Janzen 1971). In most lowland tropical forests the situation is reversed. Perhaps most important, no one tree species makes up so much of the community that it could satiate the animal community even if it were synchronized on a supra-annual basis. However, in most dipterocarp forests, either a few species, or many species in one family, constitute much of the community of adult trees.

In the temperate zones, trees on the adaptive peak of community-level predator satiation tend to have not only large seed crops, but highly edible seeds (Janzen 1971). Presumably this situation is because their fitness is higher when they produce a large number of edible seeds rather than a smaller number of slightly toxic seeds, as opposed to being on the other adaptive peak of a small number of very poisonous large seeds and satiating only specialist seed eaters that can detoxify them, as is the case with neotropical lowland forest trees on poor soil (see below). The situation is also complicated by the fact that for many mast-cropping trees in the temperate zone, some major seed predators are also dispersal agents.

Malaysian dipterocarps likewise have highly edible seeds (Browne 1955; Meijer 1969). Browne reports that on mast years in the 1940's and 1950's, 5 to 16 thousand tons of dipterocarp seeds were exported from Sarawak after being hand-gathered from the forest by indigenous peoples. They are also eaten locally, and high-quality nuts contain as much as 50 percent oil; I have found no suggestion that they contain a dramatic toxic principle, though they have a slightly resinous pericarp and may have a slight tannin content (as do acorns). Dipterocarp seeds are fed on by a wide variety of vertebrates and insects (Poore 1968; Wood 1956). However, Medway (1972a,b) very enigmatically reports that the seeds of many Malayan dipterocarps were not eaten by vertebrates at one rainforest site during

two different mast crops in Malaya. This finding suggests that either predator satiation was very effective, due perhaps to the fact that major seed-eating vertebrates such as elephants have been severely decimated, or the dipterocarp seeds are low on the vertebrates' preference list. Bearing in mind what an elephant, rhinoceros, tapir, or herd of pigs or cattle could do to the seed crop of a single dipterocarp tree, I prefer the former explanation. Harrison (1965) stresses that some of the "commonest and largest animals are predominantly or wholly frugivorous." I predict that if the oil-rich dipterocarp seed crop were dropped into an undisturbed African or neotropical rainforest growing on latosols (Bourliere 1973 reports a substantial mammal biomass in these forests), there would be no seed survival.

Is there evidence that the biomass of the seed predator community is smaller in the Malaya-Sarawak-Brunei rainforest than in African and neotropical lowland rainforests? The very fact that numerous large and highly edible seeds can lie on the forest floor long enough to generate the dense stands of dipterocarp seedlings characteristic of these forests is very suggestive. The fact that a considerable portion of the forest's seed production occurs at long intervals also implies that the animal community must be reduced, owing to the lower harvestable productivity in the "off" years. Direct evidence for low productivity would be more convincing, but except on white sand soils of Sarawak, there is none. Much of the dipterocarp rainforest is not on white sandy podzols or peat bogs. However, it is of interest that all but one of Brünig's (1973) sites used to calculate the overall species richness of trees for Borneo are sandy podzols. Therefore, on the plant side of the ledger, the evidence is very weak indeed that overall Malaysian harvestable productivity is low. About the only indication is that I and several other observers (Anderson, pers. comm.; Kellman, pers. comm.) have noted that the biomass of vines in secondary vegetation is conspicuously reduced in Malaya and Sarawak as compared to the neotropics. There is little doubt that Malaysian soils with dipterocarp forest are as poor as the latosols under other tropical lowland forests, but we don't know if they are poorer.

However, there are several suggestions that animal communities in Malaysian rainforest overall have reduced biomass as compared with large areas of African or neotropical rainforest. McClure (1966) reports a large number of species of seeds of Dipterocarpaceae and other families falling in small amounts on the Malayan rainforest floor without being eaten by vertebrates; there is no mention of the

degree to which the local animal community has been decimated by humans, but in Costa Rica, at least, even with hunters present, it would be impossible to report as McClure did. Inger (Lloyd *et al.* 1968 and included references) found much less biomass of cold-blooded vertebrates in all types of Sarawak rainforest litter than Scott (pers. comm.) found with the same methods in Costa Rican rainforest on latosols and volcanic soils. Among Sarawak amphibians and reptiles, Lloyd *et al.* (1968) also found low overall inequity and increasing inequity in the species abundance in the progression of frogs to lizards to snakes; this result is expected in an environment with low productivity. Borneo and Malaya have areas of about 780,000 and 215,000 square kilometers and have 91 and 80 species of frogs (Inger 1966). For contrast, Costa Rica with only 55,000 square kilometers has 100 species (Scott, pers. comm.). It is my opinion that the number of kinds of habitats in Costa Rica is not conspicuously larger than in Malaysia. Malaya has only 169 species of mammals and 306 species of birds (Harrison 1963) while Costa Rica has 175 species of mammals (Wilson, pers. comm.) and 758 species of birds (Slud 1964). Malaysia contains no rodents analogous in abundance and behavior to the major large seed eaters encountered very frequently on the ground in neotropical lowland rainforests (*Cuniculus*, *Dasyprocta*, *Proechimys*), though it does have a large number of species of *Rattus* and some other small rodents. Richards reports that wild game was a much larger part of the expedition's diet in British Guiana white sand sites (Davis and Richards 1933, 1934) than in Sarawak (Richards 1936; Richards, pers. comm.). Wild pigs (*Sus* spp.) in Borneo are locally highly migratory (see below), implying that there are periods when they are absent from large areas; this situation should result in an average low density of these major seed predators.

2) Why do dipterocarps wait so long between fruiting? The length of time between fruit crops is a very important parameter in satiation of seed predators. With only a couple of years between fruiting, the majority of insects that might become specialists on dipterocarp seeds are probably avoided and vertebrate populations are reduced about as far as they can be. Medway (1972a) and others have stressed that dipterocarp seeds have no host-specific insects that feed on them. However, the longer the wait between crops the larger will be the crop, and the more likely that the tree will satiate the local seed-eating animals and those that can migrate into the habitat at the time of fruiting (e.g., deer, wild ox, pigeons, pigs, people). It is of interest

to note in this context that there are 11 species of large fruit- and seed-eating pigeons in Borneo and only 5 parrots (Smythies 1960), while Costa Rica has 6 pigeons and 16 parrots (Slud 1964). Tropical pigeons commonly fly very long distances to feed on mature fruits and seeds, while parrots tend to feed locally on a very wide variety of immature seeds and mature fruits and would appear to require a steady high level of fruit availability on a local basis. These differences are reflected in the role of the passenger pigeon and European wood pigeon as major fagaceous seed predators, while the Carolina parakeet penetrated U.S. temperate-zone forests to only a small extent. Pigs in Sarawak and Malaya were famous for mass migrations prior to their exploitation by hunting (Anonymous 1953; Medway 1969; Shelford 1916). Pig migrations "occur in different places, and further information may link them with Illipe nut or some other dipterocarp seven year cycle" (Anonymous 1953). Ironically, the lower the primary productivity of the site, the longer the tree will have to store photosynthate before it has enough for a large seed crop. The variation in mast cycles from area to area may well reflect this phenomenon. In Malaya, where white sand podzols appear to be a relatively small part of rainforest soil, the period is about 6 years (e.g., Medway 1972a; Wood 1956). In Sarawak and Brunei, where white or red-yellow podzols and peat swamps are dominant soil types (e.g., Brünig 1973), periods of 9 to 11 years between heavy mast crops appear standard (Ashton 1964; Meijer 1970) though they can be shorter in some areas (Browne 1955) and may be as long as 21 years (Wood 1956).

Throughout this discussion we should note that the selection pressure for community-level synchrony is operating on fruiting time rather than flowering time. Viewed in this way, the several-month range in flowering time (Ashton 1969; Wood 1956) becomes more understandable. Different species probably have different seed-maturation times, and flowering should be synchronized only within the species to enhance outcrossing. In fact, there may well be selection for slight interspecific separation of flowering times through competition for pollinators and through competition between pollinators. Wood (1956) states that "despite the disparity in flowering times in most of the genera, the tendency was for the fruits of those that flowered late to develop faster than those that flowered earlier, so that except in a few species of *Vatica* the fruits mostly fell between mid-August and mid-October."

However, there appears to be a fair amount of

error in timing of flowering by dipterocarps (McClure 1966; Medway 1972a; Wood 1956). I suspect that this is a straightforward expression of the fact that it is impossible to have an external environmental cue that will not be damaging, yet will be sufficiently dramatic to be sensed equally by all individuals growing on sites of variable drainage, and by individuals of variable age, health, competitive status, past history, and genetic programming. Since the latter kinds of variation also occur among the branches within a single tree crown, we may also expect flowering errors to be erratically distributed in the crowns themselves. We may also expect species to have different ways of dealing with a flowering "error," such as abortion of flower buds or flowers, or even sterile fruits. All of the above responses have been reported for dipterocarps (Medway 1972a; Wood 1956).

3) How did mast fruiting evolve in a tropical rainforest? As hinted earlier, we can recognize two quite distinct possible starting points in the evolution of mast fruiting in a lowland tropical rainforest.

a) It could start with any one of the many species in a species-rich forest. In this unlikely case, the site would have to have an extraordinarily low biomass of potential seed predators. In view of the active role that seed and seedling predators probably play in maintaining habitats that are rich in tree species but do not have mast-fruiting species (Janzen 1970), such a habitat does not seem likely in the real world. However, if a mast-fruiting species were to immigrate into such a habitat, it has the potential of becoming common at the site owing to its increased numbers of seedlings relative to its neighbors. It should reduce the species richness of the site and increase the inequity of distribution of trees among the species. I would also expect that this tree would become mutually entrained with other tree species, accentuating the process. Ironically, the larger the animal community, the faster this community-level synchrony should appear, yet the effect of synchrony should be to reduce the animal community by lowering the amount of food available to it for long periods.

b) Mast fruiting could start with a species that already occurs in a nearly pure stand (owing to very severe edaphic conditions), such as *Shorea albida* forest on peat swamps (Anderson 1961, 1964a; Brünig 1964, 1968, 1969a) or a mangrove species. I feel that this is the most likely type of starting point, as supra-annual synchrony at the species level would automatically produce community-level satiation of seed predators if the habitat was large relative to other habitats from which animals could mi-

grate. Physiologically, the evolution of mast fruiting by a species would seem to involve little more than the appearance of a mutant strain of tree that requires an annual cue that is slightly harsher than usual to trigger production of flower primordia. Such a tree then produces larger seed crops in the years that it does flower and the system is in operation (Janzen 1971).

Once a mast-crop life form exists in a general region, irrespective of its origin, we may expect its ecological and evolutionary radiation into a wide variety of other habitats. It should be able to invade habitats that are richer in animal biomass than those in which it evolved, and as mentioned above it should result in the reduction of animal biomass in the invaded habitat. The latter result should be the consequence of progressively more intense selection for intra- and inter-specific synchronization as more and more of the individual trees at the site become synchronized. This observation adds significance to Ashton's (1969) discovery that trees other than dipterocarps fruit more heavily in years of dipterocarp fruiting. It is also noteworthy in this connection that fruits with small seeds (e.g., *Ficus*) that are dispersed by passing through the guts of vertebrates are not mast fruiters in the same forest (Medway 1972a).

A community rich in mast-fruiting species should display a number of interesting traits. For example, we should expect some individuals of mast-fruiting trees to act as though they were males. There may be two causes. On some occasions, a tree may respond to a flowering cue yet have only enough stored photosynthate after flower production to produce a small seed crop; it may then "make" an internal physiological decision not to use its reserves for seeds (its seeds might be eaten, for example, by even a single pig that locates the tree) but to save them for the next fruiting cycle. However, if we can assume that some outcrossing has occurred, then even a seed-barren tree has in fact reproduced in the current mast cycle. On other occasions, a particular tree may be growing on a site that is so nutrient poor that it can never make a large seed crop, or it is permanently in bad competitive straits. Here we expect it simply to flower in each mast cycle, hopefully pollinate other trees, and then abort the flowers. Facultative dioecy can very easily evolve in such circumstances. It is interesting that Ashton (1969) reports that dipterocarps occasionally flower without fruiting and that southeast Asian forests contain 20 to 25 percent dioecious tree species. It might be of value to point out that were these trees self-pollinated, there would be no adaptive value to

flowering and then aborting the flowers. It is of interest in this connection that the majority of neotropical deciduous tropical forest trees are obligate outcrossers (Bawa 1974). There is no information on the degree of facultative or obligatory outcrossing among Dipterocarpaceae, but one does wonder where the pollinators come from in a mast-fruit year. We can predict that dipterocarp flowers should last more than a day, be accessible to a wide variety of pollinator life forms, and be extremely conspicuous from a pollinator's viewpoint. Temperate-zone mast-fruiting trees are almost without exception wind-pollinated.

A second characteristic expected of forests rich in mast-fruiting species is that they should have an understory with relatively few species of shrubs and small trees that reach reproductive maturity there. This result is because most tree juveniles in such a forest will grow until they die through competition, rather than serving as food when they are seeds for a large animal community (*cf* Janzen 1972 for a discussion of this phenomenon in pure stands of *Euterpe globosa* (Palmae) in Puerto Rico). The number of dipterocarp seedlings in Malaysian forests fluctuates greatly (e.g., Barnard 1956), and since there is no evidence of major dipterocarp seedling herbivores, we must conclude that deaths are due to competition. If the canopy-member seedlings and saplings die through competition rather than being consumed as seeds, fewer resources will be available for longer-lived and shade-tolerant understory species.

A third characteristic expected of habitats rich in mast-fruiting species is that the adults, and especially juveniles, will have clumped distributions. Ashton (1969) reports this trait in mixed dipterocarp forest, and Brünig (1973) stresses it. It was very conspicuous at Bako that adult dipterocarps produce large stands of their own seedlings around their bases. Fox (1967) reported 30,000 dipterocarp seedlings per hectare (3 per m²) in a Sabah forest, and Poore (1968) reports 10,000 dipterocarp seedlings per hectare in the year after a mast year in Malaya. Fox (1967) states that in a dipterocarp forest, "seeds fall in abundance irregularly, at intervals of 3 to 6 years, normally allowing minimum development of 4,000 seedlings per acre in the subsequent year" and "70% of counted seedlings in a virgin area . . . consisted of *Shorea*, *Parashorea* and *Dipterocarpus* . . . these three species accounted for 40 percent of all trees 5 feet girth and over." Since dipterocarp seeds are gravity-wind dispersed (as expected in a forest rich in mast-fruiting species), these seedlings should be concentrated around their

parents. Once a parent is established on a site, we expect new adults to appear in her immediate vicinity, rather than at far distances as expected in an animal-rich community (Janzen 1970). I also expect this spacing pattern in habitats that have one or a few dominant tree species, but yet there are enough animals in nearby areas so that selection has favored seed escape by very toxic seeds rather than mast fruiting (see below). Large clumps of seedlings occur beneath *Eperua*, *Mora*, *Ocotea*, and *Pentaclethra* in the neotropics on white sand or other poor soils (Beard 1946; Davis and Richards 1933, 1934; Hartshorn 1973; Janzen unpub.; Richards 1952). Such aggregation also occurs when seeds escape for other reasons while still beneath the parent, such as on mammal-free Caribbean islands where it is commonplace to find dense stands of seedlings and saplings beneath parent trees even in apparently undisturbed forest.

A fourth characteristic of areas rich in mast-fruiting species should be that many of the tree species should be conspicuously site-specific. When parental replacement is set solely by competition among juveniles, the best competitors should appear to "own" any given site, and each species should become a more extreme specialist for its particular edaphic circumstances than in forests where the density of a tree species is also set by herbivory. Evolutionarily this condition should come about by the plant channeling all its resources into a maximally competitive phenotype in the context of the habitat in which it is best (e.g., raise the average seed weight without lowering the number of seeds), and by plants therefore reaching adult status only on the site where they are the very best competitors. Furthermore, as will be discussed below, the mast-fruiting tree on a different soil from that occupied by most of the population may not receive the appropriate cues and therefore may lose its seed crop by flowering out of synchrony. Ashton (1964, 1969) and Brünig (1973) have stressed and demonstrated strong site-specificity among Sarawak and Brunei dipterocarps. Kwan and Whitmore (1970) do not agree, but their analysis is based on presence/absence data rather than relative density of adult plants (and see Brünig 1973).

Strong site specificity should also be important in the physiology of mast fruiting. The larger the fraction of an adult tree population that is on one soil type, the larger will be the fraction that accumulates photosynthates at the same rate and perceives a weather event as the same cue. Viewed from the other direction, the smaller the fraction of the population that responds heavily to a fruiting cue, the

lower will be the adaptive value of intra- and inter-population synchronization for a single tree. For increased inter-population synchrony, we may note that the cue will have to be progressively more distinctive for it to be simultaneously and accurately sensed by a number of different tree species growing on different substrates over a wide area. It is therefore not surprising to find that an occasional dipterocarp species or population is out of phase with the majority of species or populations (Ashton 1969; Wood 1956). We may even expect that synchrony should evolve most easily among species on poor soil because a smaller environmental perturbation may be required there for a tree to respond than on a good soil site, where the individual trees may be more capable of buffering external perturbations with internal food reserves.

Malaysian rainforest climates are particularly suited for the evolution of mast fruiting, as they are overall very uniform yet have occasional rather severe dry spells. "Within the region of tropical rain forest, the lowlands of parts of the northern half of Borneo possess the most uniform climate" (Brüning 1969b). This appears to be the case from the viewpoint of a wide variety of organisms (Berry 1964; Berry and Varughese 1968; Foxworthy 1927; Harrison 1955; Holttum 1941; Inger and Bacon 1968; Inger and Greenberg 1963, 1966, 1967; Lloyd *et al.* 1968; Marshall 1970; Medway 1972a; Richards 1973; Seal 1958; Ward 1969; Wycherly 1968). In neotropical and African rainforests, with their conspicuous and often erratic (even when short) dry seasons, the cue for supra-annual synchrony would have to be much more dramatic (and therefore likely to be overall physiologically detrimental) than the couple of weeks of rain-free weather that dipterocarps use as a cue. A severe dry spell of the type that occurs only every couple of years in Malaysia should be an adequate cue for dipterocarps if intra- and inter-specific rates of photosynthate storage are sufficiently synchronized. A uniform climate may also lead to fairly constant rates of annual photosynthate storage, resulting in all the trees of the population responding equally to a cue.

4) Why the Dipterocarpaceae? We may start from two rather different base points in postulating why the Dipterocarpaceae are the primary mast fruiters in Malaya-Sarawak-Brunei rainforest, rather than representatives from other families. a) There may have been a number of dipterocarp species prior to the evolution of mast fruiting. Once it appeared in one species, something about the family as a whole preadapted it for entrainment to a suite of characteristics correlated with mast fruiting, for ex-

ample, commonly growing in close proximity to other trees within the same family, being chemically well protected, being especially good at living on nutrient-poor soils. b) The first species to evolve the mast-fruiting syndrome may have been especially successful on low productivity sites with uniform climates, leading to an adaptive radiation of the new life form into a variety of habitats and the production of the "family" Dipterocarpaceae. In such a reconstruction, I am in essence stating that the Dipterocarpaceae are trees that have specialized on the Malaysian physical environment coupled with bad soil. It is of interest in this connection that "the limestone soils [of Malaya] do not bear dipterocarp forest" (Ashton 1964).

I prefer hypothesis b over a, but it will be very difficult to distinguish between them. Early in the evolution of the system, the two pathways should converge strongly. It is impossible to determine which Malaysian plant families could produce a major radiation of mast-fruiting species, though we might expect it to appear in one of those families with vegetation that is chemically very well protected and that constitutes a large part of the forest biomass for reasons other than being a mast-fruiting species (e.g., Anacardiaceae, Casuarinaceae, Ericaceae, Euphorbiaceae, Guttiferae, Lauraceae, Myrtaceae, Pinaceae, Podocarpaceae, Theaceae).

Finally, we are confronted with the question of why bad soil sites may have led to the evolution of mast fruiting in Malaysia, yet in the neotropics and mangrove swamps large poisonous seeds appear to be the primary reproductive strategy in forests with low tree species richness (see section IV). The answer may lie in the productivity of the vegetation, and hence animal biomass, near the site of low productivity, and the size of the low productivity site relative to the areas of higher productivity. For example, if a neotropical mangrove species were magically converted to a mast-fruiting species overnight, we could expect a mass migration of a diverse and large animal community into the mangrove forest at the time of seed production. It seems doubtful that a strip of mangroves a few hundred meters wide could come anywhere near satiating the large animal community found in the forest on latosols on slightly higher ground. The same argument may be applied on a larger scale to the British Guiana white sand and other edaphic vegetation types described by Davis and Richards (1933, 1934), and the Costa Rican *Prioria* and *Pentaclethra* forests to be discussed in section IV. The mystery remains, however, as to why the extensive Rio Negro drainage basin has not developed mast-fruiting species.

As will be remembered from previous discussion of the cues needed for supra-annual mast fruiting, it may be that South America does not offer a weather regime of the appropriate type.

Mast fruiting occurs in a few other types of tropical woody plants, and the bamboos are one of the most conspicuous. These forest grasses have large seeds which are highly edible (as appears to be the case for virtually all grasses). Perhaps the most dramatic case is that of Indian bamboos which are on a flowering cycle of 15 to 45 or more years. There is no suggestion that they are associated with regions of low primary productivity unless they are understory plants, and it is not obvious how the system became started. However, once started, it is fairly easy to visualize how the flowering cycle became so long, especially if humans have been involved as seed predators. If the bamboo is to satiate the local animal populations, it must have a large seed crop. To produce a large seed crop requires a long period of photosynthate storage. However, if the plant is to wait a long time, it must use a very intense cue for flowering (i.e., the weather event must be rare and conspicuous). A severe drought is about the only such cue available in a tropical area. However, when there is a severe drought, there are large numbers of starving animals, including humans. This result means that seed predation will be exceptionally heavy in the year of the flowering cue. Small wonder that the fruiting of the bamboo is regarded as a spiritual salvation to relieve the starvation caused by exceptionally bad droughts (Blatter 1929, 1930a,b; Santapau 1962). The same process is probably operative with *Strobilanthes* (Acanthaceae) with its 12-year gregarious flowering cycle in southern India (Matthew 1959, 1971; Robinson 1936; Steenis 1942); it is noteworthy that *Strobilanthes* is one of the two major understory plants in the low-diversity evergreen sholas forest of India mentioned in section IV (Lakshmanan 1968).

IV. FORESTS WITH LOW SPECIES RICHNESS

The previous discussion of forests rich in mast-fruiting Dipterocarpaceae leads immediately to thoughts about other tropical lowland evergreen trees that occur in stands where most of the large trees belong to less than about five species. The existence of such forests and the existence of dipterocarp forests falsify the dogma that diversity is mandatory for ecosystem stability in highly equitable climates.

These forests are thus very worthy of special scrutiny. With respect to seeds, most tropical lowland for-

ests with low vegetative diversity may be placed in two categories. Either they are mast fruiting, or they rather continually produce large and toxic seeds, or seeds that are individually especially well protected in some other manner. Tannin-rich mangrove seeds, or seedlings in the case of *Rhizophora*, are a well-known example of the toxic seed category, but there are many others. Judging from my observations that rodents and insects on the Osa Peninsula (Costa Rica) do not attack the huge seeds of *Mora oleifera*, the *Mora* species (Leguminosae) that constitute large portions of the canopy in several Guiana and Trinidad swamp forest types (Beard 1945, 1946; Davis and Richards 1933, 1934) and on Suriname white sand soils (= *Dimorphandra*, Stark 1970) have very poisonous seeds. Fittkau (pers. comm.) reports the same for *Mora* on the Rio Negro. Brazilian *Mora* (= *Dimorphandra*) pods contain 8 percent rutin, a pharmacologically active flavone (Mors and Rizzini 1966), and large amounts of a dark red dye can be leached from *Mora oleifera* seeds. They appear to be very rich in alkaloids (E. A. Bell, pers. comm.). Beard (1946) reports that the seed contents can be eaten by humans if they are first ground and leached in water. In British Guiana and Trinidad, *Mora* produce dense stands of seedlings around their bases, a characteristic implying freedom from animal attack. The same high production of seedlings has been described for *Ocotea* and *Eperua* forest (Davis and Richards 1933, 1934; Takeuchi 1961, 1962a,b). *Eperua* flowers are extremely showy (Ducke 1940), and it seems unlikely that supra-annual mast flowering would have gone unobserved. As these and other authors have given no hint of mast fruiting by these species, it seems a reasonable inference that *Ocotea* and *Eperua* seeds will be found to be very toxic. *Pentaclethra macroloba* (Leguminosae) may make up as much as 40 percent of the canopy over some Costa Rican rainforest swampy soils (Hartshorn 1973), and is one of the most common subdominants on British Guiana white sand soil sites (Richards 1952) and in Trinidad *Mora* and other forests (Beard 1946). It has 5- to 10-gram seeds (fresh weight) that are ignored by almost all species of rainforest rodents and almost all insects (unpub. field notes). *Pentaclethra macrophylla* seeds in Africa are rich in an unidentified alkaloid (Pammel 1911), and *P. macroloba* seeds contain high concentrations of an unidentified alkaloid (Bell, pers. comm.). *Prioria copaifera* (Leguminosae), which forms nearly pure stands in coastal swamp forests of Costa Rica (Allen 1956), has large seeds in an indehiscent pod, with tannin-rich walls. *Raphia* and

other palms form dense stands in fresh-water swamps in Africa and the neotropics (Richards 1952); while their seeds appear to contain no toxic compounds, at least in Costa Rica they fall into water and sink to the bottom where they are unavailable to most animals (unpub. field notes). While unexplored ecologically, tropical forested swamps are well known commonly to contain monospecific stands of trees, for example, *Pterocarpus officinalis* (Gonggryp and Burger 1948), *Parkinsonia aculeata* in swamps in Costa Rican deciduous forest (unpublished field notes), *Erythrina glauca*, and *Machaerium lunatum* (Lindeman 1953). It seems quite reasonable that in addition to being vegetatively well protected, these plants have seeds protected during part or all of the year by the water. It would not be surprising to find that some of the dipterocarps that form low-diversity forests in animal-rich areas have toxic seeds and reduced mast-fruiting behavior. It is of extreme interest in this context that *Shorea robusta*, which forms extensive deciduous forests in India, has exceptionally tannin-rich seeds (Burkill 1935) and apparently bears seed every year (in contrast to the Indian bamboos with their highly edible seeds and long mast cycles).

It is among tree species with large and toxic seeds that we might expect to find species that fruit annually and even more than once during the year. *Mora* forests bear fruits every year (Beard 1946), *Prioria copaifera* fruits irregularly throughout the year (Allen 1956), and Costa Rican *Pentaclethra macroloba* forest has several distinct fruit-bearing periods during the year (Hartshorn 1973).

If the seeds are very well protected, then any synchrony that does occur within the year should be set by constraints on pollination or the timing of seed germination. It is not surprising to find that mangroves in Costa Rica flower during much of the year, as they are insect-pollinated and thus conspecifics need not be shoulder to shoulder to insure cross-pollination; since new sites for colonization are available most of the year, fruit-bearing should be continuous. On the other hand, it is of interest that in the same region, the mangrove *Avicennia nitida* has a highly synchronized flowering period (Allen 1956) toward the end of the time when many other trees in the adjacent dry-land forest are in flower (Janzen 1967). *Mora oleifera*, growing in a narrow strip along the landward margin of Pacific Costa Rican mangrove swamps (Allen 1956), drops its huge seeds (up to one-half kilogram) just before the highest spring tides. The seeds are then floated and deposited just slightly ocean-ward from the parent trees (unpub. field

notes).

A rainforest animal community may be severely reduced in ways other than low primary productivity at the site. Small islands commonly have forests with low tree-species richness within a given habitat, and they have severely reduced biomass and species richness of native herbivores (Janzen 1973b,c). Since a low habitat diversity on an island is not subject to potential invasion from adjacent habitats with high animal biomass, I expect plants to be able to grow in pure stands concomitant with relaxed selection for exceptional chemical defenses. This conclusion is suggested by the extreme ability of introduced mammals to decimate natural island floras (e.g., Howard 1967), and the observation that the forests of low diversity on tropical islands are not generally noted for commercial harvest of resins or other toxic secondary compounds. On tropical islands, we may also expect satiation of seed predators at the community level, as is the case in the *Euterpe globosa* palm forests of Puerto Rico (Janzen 1972). If there are no seed predators, then we expect a total lack of synchrony in fruit maturation and the production of a few huge and highly edible seeds, as is the case with the palm *Lodoicea maldivica* which grows in nearly pure stands in Seychelles Islands and has the largest seed in the world (McCurrach 1960). It is noteworthy in this context that the Philippines, Java, etc. are island communities, and the success of dipterocarps in their forests (Brown and Brown 1914; Serevo 1960; Slooten 1952; Whitford 1906) may be related to a reduction of animal communities among their vegetation for this reason, rather than due to poor quality soil.

With respect to the foliage, it is not only white sands that bear evergreen and monotonous vegetation that is particularly rich in secondary compounds. It appears that this is a general characteristic in habitats with very low primary productivity yet a climate favorable to animals. This is another way of saying, "in those habitats where the loss of a leaf causes a very great depression in plant fitness." The understory shrubs of evergreen lowland tropical rainforest are low in diversity when compared with the canopy and are a major source of spice-rich plants, have very reduced foliage-inhabiting insect biomass (Janzen 1973a,b), and appear on other grounds to have highly toxic foliage with a low rate of replacement (e.g., Bourliere 1973 stresses that rainforest vertebrates live almost entirely on canopy foliage or material that falls from the canopy). The evergreen ericaceous shrubs in the understory of eastern United States deciduous forest have highly

toxic foliage (e.g., Forbes and Bechdel 1931; Pammel 1911) and long-lived leaves (Monk, pers. comm.). *Melaleuca* (Myrtaceae) forms large pure stands on acid, saline, or waterlogged soils in Malaya (Johnson 1967a), and its leaves are distilled for medicinal compounds. The pure stands of evergreen oaks (*Quercus* spp.), Lauraceae, and Ericaceae at high tropical elevations are probably protected from insect outbreaks by tannin-rich foliage just as are their temperate-zone relatives (Feeny 1968, 1969; Hathaway 1958) in forests of low diversity. The large pure stands of *Quercus oleoides* in the lowlands of Central America, usually on the worst soils of the region, are in the same category. In the evergreen-stunted Indian hill forest "sholas," the dominant tree families are Lauraceae, Myrtaceae, and Syracaceae with an understory of Rubiaceae and Acanthaceae (mast-fruiting *Strobilanthes* sp.); the dominant tree species belong to the Elaeocarpaceae, Euphorbiaceae, Flacourtiaceae, Magnoliaceae, Myrtaceae, Sapotaceae, Theaceae, and Thymelaeaceae. When denuded, sholas are occupied by nearly pure stands of myrtaceous or anacardiaceous shrubs (Lakshmanan 1968). As mentioned in the first section of this paper, *Mora* has especially durable wood (Allen 1956; Gonggryp and Burger 1948), and is a local commercial tannin source in Brazil (= *Dimorphandra*, Mors and Rizzini 1966). *Pentaclethra* has wood especially rich in tannins, and *P. macroloba* logs lie on the rainforest floor for many years before decomposing (Hartshorn 1973). *Prioria copaiifera* wood is famous for exuding copious tannin-rich black gum when cut (Allen 1956; Mors and Rizzini 1966; Pammel 1911), and *P. copaiifera* swamp forest in Panama was found to have the lowest caloric input of litter per hectare of six Panamanian rainforest types examined by Woods and Gallegos (1970). *Copaifera* (Leguminosae), another major resin producer, is a common small tree in Sarawak *Shorea albida* peat swamp forest (Anderson 1961; Burkill 1935). *Protium copal* (Burseraceae) is the second most common dicot canopy-member tree in the Costa Rican *Pentaclethra* forest mentioned above (Hartshorn, pers. comm.) and produces excessive amounts of resin (Allen 1956). Species-poor stands of desert perennials are notorious for toxicity. It is no accident that the temperate-zone evergreen conifer forests are rich in resins and other secondary compounds.

Mangroves, with their extraordinarily high tannin content (e.g., Allen 1956; Burkill 1935; Fosberg 1945; Nierenstein 1934; Pammel 1911; Standley 1920-1926), are perhaps an extreme case. As recently demonstrated in Viet Nam, a single defolia-

tion of mangroves with chemicals is usually lethal to the tree, yet mangroves display some of the highest primary productivity of any forest (Golley, pers. comm.). It is tempting to postulate that the very conspicuous chemical defenses of mangroves are not only to avoid attack by marine animals, but to minimize the possibility of a mangrove being defoliated by herbivores. Frequent defoliation would be almost certainly unavoidable if the leaves in such a low-diversity evergreen foliage were highly edible. Their extreme sensitivity to defoliation could well be because the ever-present leaves are crucial in physiologically avoiding salt damage. Incidentally, if tidal flux did not result in frequent leaching and washing of litter out of the system, we would expect mangrove swamps to generate blackwater rivers. Indeed, a southern Mexican non-tidal mangrove swamp has been described as having a peat bog beneath it (Thom 1967).

The above comments should not be taken to imply that some species of evergreen trees on good soil will not be well defended or that deciduous species-rich forests will be devoid of species with chemically well-defended vegetative parts. Scattered through Costa Rican deciduous forest are evergreen tree species, which, if grown in a pure stand, would probably produce an ortstein, a podzol, and/or a deep litter layer. For example, *Hymenaea courbaril* (Leguminosae) produces copious amounts of resin (Burkill 1935; Langenheim 1973; Standley 1920-1926) and has extremely resinous and sclerophyllous leaves that remain on the tree about 11.5 months of the year. *Manilkara chicle* (Sapotaceae) is well known for its large quantities of latex (chicle of commerce) as are the evergreen figs (*Ficus* spp.). *Andira enermis* (Leguminosae) has bark and seeds that were used for a "pugative, vermifuge, febrifuge or anthelmintic but large doses are said to be dangerous, producing delirium or even death" (Standley 1920-1926). *Byrsonima crassifolia* (Malpighiaceae) has bark used for tanning and dyeing and "the plant is astringent" (Standley 1920-1926). *Curatella americana* (Dilleniaceae) has bark "rich in tannin and is used in Brazil for tanning skins" (Standley 1920-1926). The leaves of all of these evergreens are conspicuous in being almost entirely free of insect damage throughout the year. *Bursera simarouba* (Burseraceae) is another common tree in these forests; it is deciduous, but has a conspicuous green photosynthesizing layer directly under the stem epidermis and so is effectively evergreen. *B. simarouba* and congeners are prominent producers of medicinal gums, and "the Caribs employed it for painting their canoes to preserve them from the attacks of worms"

(Standley 1920-1926). *Jacquinia pungens* (Theophrastaceae), an understory shrub in the same forests, is an extreme case. It bears leaves only during the dry season, thus earning the misnomer "siempre verde," suffers virtually no defoliation, and has foliage rich in fish poisons (Janzen 1970).

Throughout this paper, I have talked as though the foliage of the common tree species in low-diversity tropical forests is nearly free of insect attack. In general, this appears to be the case, but there are a few recorded cases where apparently host-specific insects defoliate large areas of one species (Anderson 1961; Atkinson 1953; Gray 1972; Kalshoven 1953; Kapur 1958). The general explanation appears to be that some combination of weather events leads to exceptionally good reproduction of the herbivores. Severe defoliation follows before the insects eat all their host's leaves, have weather events depress their population, and/or parasites/predators build up on them. In this sense they appear to differ in no significant way from the analogous interaction in temperate-zone forests of low foliage diversity. Furthermore, it is likely that such defoliation leads to a delay or failure in production of mast seed crops at a later date, just as is the case in temperate-zone forests. In one example, it appears that a single defoliation by moth larvae (Lymantriidae) killed 12,000 hectares of *Shorea albidia* forest with 400-480 trees per acre (Anderson 1961). Again, as in temperate-zone forests, I suspect that upon more detailed examination, we will find that herbivore outbreaks in dipterocarp forest occur at the time of production of new foliage or when the trees are weakened, rather than the trees being generally susceptible to insect attack.

DISCUSSION

The patterns dealt with here are not absolute categories. For example, a white sand soil need not generate a blackwater river, if the vegetation happens to be made up of species that use solely alkaloids for their defense against herbivores. A nutrient-rich soil may produce blackwater rivers if it becomes colonized by exceptionally tannin-rich species of plants. On the other hand, toxic foliage falling on exceptionally nutrient-rich soil may be competently degraded by the litter fauna, for example, see the discussion of the biogenesis of mull and mor soils by Handley (1954); the same argument applies to the blackwaters themselves, and we must remember that what is toxic on an empty stomach is just flavoring on a full stomach. Immigration of an aggressive mast-fruiting species of tree into a habitat may reduce the animal community even if the soil

quality is high.

A particularly conspicuous problem in the variability of interaction of well-protected plants and white sand soils is that much of the Brazilian white sand and other nutrient-poor soils (Goodland 1971) bear a low scrubby vegetation ("campo," "caatinga"), yet some of this does not appear to have an ortstein or even particularly dark deep humus layer (Arens 1963; Eiten 1963; Ferri 1960; Heyligers 1963; Sioli 1967; Spruce 1908; Stark 1970). These sands do, however, produce blackwater rivers. Some of this vegetation differs from the forest on the white sand soils of Sarawak, British Guiana, and Suriname in that it is occasionally burned. It is possible that a major part of the secondary compounds is lost through fire consumption of the litter rather than leaching by rainfall. This process also appears to be occurring in *Pentacme* (Dipterocarpaceae) forest on sandy soil in India (Ogawa *et al.* 1961). In fire-rich habitats we also expect the evergreen life form to be less prominent, as retention of leaves during the dry season raises the chances of losing a major part of one's nutrient reserves to the capricious herbivore fire. As the proportion of deciduous leaves rises in a tropical habitat, I expect that the absolute amount of secondary compounds in the litter and rainfall leachate will decline.

In bringing this paper to a close, it seems appropriate to comment briefly on some broader aspects of tropical ecology that it has brought to mind.

1) If the degree of evergreenness is an adaptive response to nutrient-poor soils, then the implications behind words such as "evergreen rainforest" and "sclerophyll scrub" should be subject to very close scrutiny.

2) If the rates of tropical vegetation replacement following fire or other perturbation really vary as much as they appear to over soil and elevational gradients, then attempts to describe and classify vegetation on low productivity sites seem especially futile; apparently "climax" vegetation may be the result of a fire two hundred years before, and in fact only be in the early stages of succession.

3) Low-diversity forests are commonplace in the tropics; apparently stable, they should lead us to search for the natural processes that lead to herbivores not building up on a food supply that appears unlimited to the appropriate specialist.

4) Litter depth should not be directly related to the productivity or the rate of litter input to a site, since it must be disappearing at the same rate that it is coming in. However, litter depth should be directly related to how long the litter has to lie on the

soil being leached by the rain, before its toxin content has fallen to the point where the litter fauna and flora can go to work on it.

5) From an animal's viewpoint, changes in productivity do not necessarily produce corresponding changes in available food; what counts far more is what the plant does with, for example, additional photosynthate, or how it re-allocates its resources when its overall productivity is lowered. A tropical rainforest might easily have three times the primary productivity of a temperate-zone forest, yet have only a tenth as much harvestable productivity from a herbivore's point of view. Seen the other way round, two tropical evergreen forests of the same standing crop may have drastically different productivities from the animals' viewpoint and, of course, very different primary productivities as well.

6) Toxicity of any compound is a relative thing. For example, on a nutrient-rich soil, a tree with very toxic leaves may have no effect on the litter fauna and soil-forming processes, while on a nutrient-poor site, a mildly toxic tree may have a huge effect.

In conclusion, it seems appropriate to point out that the type of analysis applied in this paper could be of use in understanding the dynamics of the development of temperate-zone peat bogs and their blackwater rivers (Conway 1949; Gimingham 1972; Gorham 1957; Heinselman 1963, 1965; Hutchinson 1957; Reader and Stewart 1972; Small 1972a), as well as temperate podzols and mors (Burgess 1965; Dimpleby 1962; Handley 1954; Ponomareva 1969; Rode 1970; Skoropanov 1968; Waksman 1938). For example, many extra-tropical bog and mor organics have extremely low decomposition rates (e.g., Douglas and Tedrow 1959; Gorham 1957; Kendrick 1959; Perrin *et al.* 1964; Reader and Stewart 1972); if a bog is alternately drained and flooded, its woody plants will be replaced by fast-growing and often deciduous species that are not especially noted for toxic foliage (e.g., Gorham 1957; Lloyd and Scarth 1922). Presumably the changes in water level are repeatedly flushing out secondary compounds and oxygenating the substrate so that fungi and bacteria can decompose the phenolics and other toxic chemicals. A second example is provided by the observa-

tion that conifers and ericaceous shrubs on temperate-zone peats are very slow-growing plants, have foliage rich in toxic secondary compounds, and leaves with a long life span (Forbes and Bechdel 1931; Harley 1952; Knerer and Atwood 1973; Muen-scher 1970; Pammel 1911; Tamm 1955; Williams 1970; etc.). They also possess "sclerophyllous" leaves which are generally interpreted as either adaptations to some as yet undiscovered type of physiological drought or to direct "symptoms" of nutrient deficiency (e.g., Arens 1963; Brünig 1969b; Loveless 1961; Small 1972a). By way of rebuttal, I would simply like to emphasize my strong agreement with Ponomareva (1969: 257) when she stated, "Coniferous tree species, each year shedding only part of their needles, perennial subshrubs, evergreen plants, etc. are all adaptive forms of live nature to conditions under which mineral nutrients are strongly leached out of the plant's environment," and add, "imagine what would happen to an evergreen bog during the winter if the foliage were highly edible to deer."

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This study is dedicated to those unfortunate tropical farmers whose governments cause them to attempt to survive on white sand soils either because they appear unexploited or for political reasons.

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